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THE EVOLUTION, HOST RELATIONSHIPS AND CLASSIFICATION OF THE NEMATODE SUPERFAMILY HETERAKOIDEA

WILLIAM G. INGLIS

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THE EVOLUTION, HOST RELATIONSHIPS AND CLASSIFICATION OF THE NEMATODE SUPERFAMILY HETERAKOIDEA

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NATURAL HISTORY

BY

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THE EVOLUTION, HOST RELATIONSHIPS AND CLASSIFICATION OF THE NEMATODE SUPERFAMILY HETERAKOIDEA

By WILLIAM G. INGLIS

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APOLOGIA

Several years ago I published a classification of the nematode Superfamily Heterakoidea (Inglis, 1958) but presented no justification as I always hoped to produce a full revision. It has become increasingly clear that this is never likely to be completed largely because of a shift in my interests in conjunction with a lack of material on which to base such a revision. I therefore present here reasons for the classification previously proposed and regret being unable to complete the whole work. No illustrations are given as they can be found in Skrjabin, Schikhobalova and Lagodovskaja (1961) and Chabaud (1965).

SYNOPSIS

The comparative anatomy of the Superfamily Heterakoidea is described and the morphological sequences recognized are used as the basis for the classification proposed. The evolution of the superfamily is interpreted in terms of (1) intra-host localisation; (2) major host groups (i.e. amphibia, reptiles, birds and mammals); (3) the feeding habits and ecology of the hosts; and (4) geographical restriction. The superfamily is classified into three families, five subfamilies and fourteen genera, thus: Heterakidae: Heterakinae (*Heterakis*, *Odontoterakis*, *Pseudaspidodera*); Meteterakinae (*Meteterakis*, *Gireterakis*); and Spinicaudinae (*Spinicauda*, *Africana*, *Moaciria*, *Strongyluris*). Aspidoderidae: Aspidoderinae (*Aspidodera*, *Ansiruptodera*); and Lauroiinae (*Lauroia*, *Paraspidodera*). Ascaridiidae (*Ascaridia*). A key is given to the genera of the superfamily. The following genera are not accepted largely because the morphology of the specimens does not correspond to the published descriptions, thus: *Preterakis* Freitas, 1956; *Heterakoides* Freitas, 1956; *Pareterakis* Freitas, 1956; *Pseudaspidoderoides* Freitas, 1956; *Pseudaspidoderina* Freitas, 1956; *Raillietakis* Freitas, 1956; *Sexansodera* Skrjabin & Schikhobalova, 1947; *Bellaplectana* Skrjabin, Schikhobalova & Lagodovskaja, 1961; *Spinaspidodera* Skrjabin & Schikhobalova, 1947; *Ganguleterakis* Lane, 1914; and *Cheloniheterakis* Yamaguti, 1961.

INTRODUCTION

No full revision of the Heterakoidea or Heterakidae has ever been carried out although several groupings have been proposed largely based on other published work. However, Travassos (1913) did produce a partial revision based largely on the species occurring in Brazil. Other minor changes in the classification were proposed later but no major alterations were suggested for almost thirty-five years when Skrjabin & Schikhobalova (1947, 1947*a*), Freitas (1956), Inglis (1957, 1958) and Chabaud (1957) all advanced new groupings. Most recently the superfamily has been re-grouped once more by Skrjabin, Schikhobalova & Lagodovskaja (1961) and by Yamaguti (1961).

All the classifications proposed, except my own, have been based on biblio-taxonomic studies while the results presented here are based on a study of virtually all the type material available in the world's collections together with a study of many other specimens.

In anticipation of the discussion that follows it may be stressed that the following genera proposed by Freitas (1956) and Skrjabin *et al.* (1961) cannot stand because the descriptions they classify are contradicted by the morphology of the specimens, thus: *Bellaplectana* Skrjabin *et al.*, 1961 is a synonym of *Moaciria* since *Aplectana pharyngeodentata* Belle, 1957 (of which I have studied the type series) does not possess the so-called teeth in the buccal cavity on which the genus is based. These structures are simply the retracted lips, a common artefact in poorly preserved *Spinicauda* and *Moaciria* species. *Preterakis* Freitas, 1956 falls as a synonym of *Africana* because the fusion of the caudal alae on the male tail on which it is based does not occur. Such an apparent fusion occurs in many specimens of the superfamily but is an artefact due to contraction during fixation and even the artefact does not occur in all the specimens of the type series of *Africana astylosterni* Sandground, 1933. As a consequence the subfamily Preterakinae Freitas, 1956 must also disappear.

Finally the following genera proposed by Freitas (1956) are not accepted by Skrjabin *et al.* (1961) nor by myself, thus: *Heterakoides* Freitas, 1956 since, although *Spinicauda triaculeatus* Kreis, 1933 is certainly slightly different from the other species referred to *Meteterakis* (Inglis, 1958*a*) I still do not feel it warrants generic separation. Similarly the genus *Pareterakis* Freitas, 1956 is a synonym of *Meteterakis* since there are no characters which allow it to be distinguished. *Pseudaspidoderoides* falls because the anastomozing cordons reported by Chakravarty (1938) appear to be due to contraction of the type specimens, which I have seen.

COMPARATIVE ANATOMY OF THE SUPERFAMILY

All the species referable to the Superfamily, with the exception of the genera *Ascaridia* and *Lauroia* which are discussed later, have the following features in common. The head bears three large, distinct lips, the detailed structure of which varies throughout the family and has been considered elsewhere (Inglis, 1957). In summary, however, the dorsal lip carries two doubled papillae and each ventro-lateral lip carries a single ventro-lateral doubled papilla and a single lateral papilla associated with the amphid. The inner surface of each lip carries an anterior flange which varies in relative size throughout the superfamily. The head in *Lauroia*, which I did not deal with before, is typical of this pattern with lobes connecting the lips. It is, however, characterized by the development of three plate-like regions posterior to each lip. This is clearly a development of cordons from one source (see particularly Proença's (1938) figures of *L. travassosi*) comparable to the condition in *Gireterakis*. In *Ascaridia* the lips are large and stout but otherwise typically Heterakoid.

The anterior region of the oesophagus is divided into three separate anterior lobes, previously called " pharyngeal portions ", at the tip of each of which is a cuticular onchium, except in one case. From studies completed since 1957 it now appears that the lips are operated by a system of fibres which are not arranged in a septum as in the Ascaridoidea (Inglis, 1965) but this has not been fully analysed. In addition in the Heterakinae there is generally a pair of lateral papillae lying on the body just posterior to the lip region.

The oesophagus, except in *Ascaridia*, is modified anteriorly into a short region generally called a pharynx and swells fairly evenly posteriorly to form a bulb-like region, containing three valves, which is not clearly offset from the remainder of the oesophagus by a constriction. The distinction between the pharyngeal region, the bulb and the remainder of the oesophagus is the presence of marginal tubes in the radii of the lumen of the oesophagus in the intervening length between the bulb and pharynx. Into these marginal tubes project a series of paired leaf-like cuticular structures and this arrangement gives the oesophagus its typical longitudinal doubled appearance.

The oesophagus is relatively long and narrow with a markedly small posterior bulb in *Aspidodera*, *Ansiruptodera*, *Lauroia* and *Paraspidodera*; the oesophagus is less markedly narrow in *Africana*, *Gireterakis*, *Meteterakis*, *Moaciria*, *Spinicauda* and *Strongyluris*, and is relatively short and stout in *Heterakis*, *Odontoterakis*, and *Pseudaspidodera*. The oesophagus is club-shaped without a posterior bulb in *Ascaridia*. The nuclei of the ventral oesophageal glands are doubled.

Lateral alae, which may be prominent in the cervical region, are typically present. They are relatively broad in *Heterakis*, *Odontoterakis*, *Pseudaspidodera* and *Gireterakis*; are present but relatively narrow in *Africana*, *Spinicauda*, *Moaciria* and *Strongyluris*—in which genera the lateral fields are very prominent—and also in *Meteterakis* and *Ascaridia* but they are lacking in *Aspidodera*, *Ansiruptodera*, *Lauroia* and *Paraspidodera*.

The nerve ring encircles the oesophagus about one third of its length posterior to the pharynx and the excretory pore opens just posterior to the nerve ring.

Small sessile papillae are borne on the general body surface in *Africana* (few), *Meteterakis* (few), *Spinicauda* (very few), *Moaciria* (many) and *Strongyluris* (many). Such papillae are, however, frequently difficult to see and they are probably more easily seen in *Strongyluris* species because such species are relatively larger than the others.

The Male Tail

A circular pre-cloacal sucker with a cuticular rim is always present (except in *Lauroia*). Caudal alae are fairly common in the superfamily and, when present, never meet on the ventral surface of the body anterior to the pre-cloacal sucker. In those specimens in which the tail has contracted during fixation such a junction may appear to exist but it is clearly an artefact and is, therefore, of no use as a systematic character. Freitas (1956) lays considerable stress on this " junction " of the caudal alae, going so far as to use it to differentiate genera. I would stress that not only is this an artefact but it is not present in all the specimens of most of the species of which it is considered a diagnostic character.

In the genera *Heterakis*, *Odontoterakis* and *Pseudaspidodera* there are, typically, eleven pairs of caudal papillae, of which seven pairs are long and support broad caudal alae. Two pairs of these papillae, which are always slim, flank the pre-cloacal sucker, four pairs lie lateral to the cloacal opening (later referred to as the para-cloacal papillae), and one pair lies posterior to the cloacal opening, roughly midway between the para-cloacals and the terminal spike of the tail. The remaining four pairs of papillae are typically sessile, two pairs flank the cloacal opening, the peri-cloacal papillae, of which one pair is pre-cloacal and one pair post-cloacal. The remaining two pairs of papillae lie at the base of the terminal spike of the tail with one pair wholly ventral and one pair lateral in position. The phasmids open just anterior to the terminal group of ventral papillae and have generally been described as papillae. In some cases additional papillae occur, in particular a pair of sessile papillae frequently occur anterior to the suctorial pairs and an additional long pair sometimes occurs immediately posterior to the para-cloacals.

The tail ends posteriorly in a long, narrow, evenly pointed, non-alate terminal spike. In all four genera the pre-cloacal sucker is relatively large and there is no gubernaculum.

Both *Spinicauda* and *Africana* have long narrow tails bearing many small sessile papillae and a relatively small pre-cloacal sucker. There are no caudal alae in *Spinicauda* while those in *Africana* stop posteriorly at the level of the cloacal opening and are unsupported by papillae. A gubernaculum is present in *Spinicauda* and a gubernacular mass in *Africana* (gubernacular mass is a term proposed earlier for the strongly cuticularized lining of the cloaca in the genus *Meteterakis* (Inglis, 1958*a*)).

The tail in *Strongyluris* is very short with a large pre-cloacal sucker which is directed posteriorly. The caudal alae are very broad and are typically supported by seven pairs of long stout papillae of which the largest are the three most anterior pairs, with the others becoming increasingly smaller posteriorly. There are, in addition, two pairs of ventral sessile papillae peri-cloacal in position and one similar pair just anterior to the beginning of the terminal spike. There is no gubernaculum. The tail in *Moaciria* is similar but with a long terminal spike and a gubernaculum.

The relatively long, narrow tail in *Meteterakis* is characterized by a small pre-cloacal sucker and narrow caudal alae supported by, typically, three, exceptionally four, pairs of short, stout papillae of which, typically two pairs, exceptionally three pairs, lie about the level of the pre-cloacal sucker and the remaining pair is roughly at the level of the cloacal opening. There are in addition many pairs of small sessile papillae (up to about twenty) on the tail which may represent the caudal complement of the similar papillae which are found scattered generally over the surface of the body. A gubernacular mass is present in all except one (possibly two) species. The tail in *Gireterakis* is very similar to that of *Meteterakis* with the same three pairs of swollen papillae supporting the caudal alae but there are much fewer small sessile papillae and there is no gubernacular mass.

The tail in the genera *Aspidodera*, *Ansiruptodera*, and *Paraspidodera* is so uniform that one description will cover all three. It is long and thin, tapering evenly to a point. It has no caudal alae, the pre-cloacal sucker is markedly small and there is a large number of small sessile papillae arranged in roughly parallel rows. A gubernaculum is present in all three genera.

The tail in *Lauroia* is highly modified but may be interpreted as being derived from a tail similar to that characteristic of the previous three genera by a great reduction of all its structures. Thus the pre-cloacal sucker is represented by a slight swelling and the number of sessile caudal papillae is very small.

The tail in *Ascaridia* is relatively stout with narrow alae supported by short stout papillae. The pre-cloacal papillae are sessile and there is no gubernaculum.

The Spicules

The spicules are always equal in length, non-alate, simple and identical in structure in the genera *Africana*, *Ascaridia*, *Aspidodera*, *Ansiruptodera*, *Moaciria*, *Paraspido-*

dera, *Spinicauda* and *Strongyluris*. They are equal in length and identical in structure, with alae in some cases, in *Meteterakis* and *Africana*. They are equal in length and slightly elaborate although identical in structure in *Gireterakis* while in *Heterakis*, *Odontoterakis* and *Pseudaspidodera* they are frequently unequal in length and may be very dissimilar in *Heterakis* and *Pseudaspidodera* but are always simple, needle-like in *Odontoterakis*. It may be noted here, and will be referred to later, that the general facies of the male tail in *Aspidodera*, *Ansiruptodera*, and, to a lesser extent, *Paraspidodera* is remarkably uniform even to the same general shape of the spicules which are, almost invariably, rather stout with squarish ends.

SYSTEMATIC GROUPS WITHIN THE SUPERFAMILY

This section should be read in conjunction with the discussion of morphological trends given in the next section, since the classification presented reflects the sequences discussed there. In other words this classification is largely *akoluthic* (sensu Inglis, 1966*a*) in reflecting trends in morphological modification rather than in attempting to assess over-all resemblances or simply utilizing key characters. It does appear, however that an assessment of over-all resemblances would produce a classification the same as the present since virtually the only characters available for analysis are those of the head and the male tail and a classification based on either alone is congruent with one based on the other. That is, if only tails are classified they fall into roughly the same major groupings as do the heads if classified alone. This explanatory discussion of procedure intrudes here because in classifications such as this I find it impossible to separate the discussion of the process of classification from that of the establishment and recognition of morphological trends. In fact the trends were probably recognized before the classification was developed. It is, however, easier to follow the discussion of trends and host relationships if a foundation is given upon which they can be discussed.

As stressed above most classifications of this superfamily (family) have been mainly based on published descriptions which are in many cases incomplete or inaccurate. A reliable assessment of such descriptions, and the characters upon which to form a classification can only be made after a wide and detailed knowledge of the group under consideration has been obtained. The dangers involved in bibliotaxonomy are exemplified by the gross oversplitting proposed by Freitas (1956) with a multiplicity of new names at all levels of taxa. The classification proposed by Freitas may be considered analytical in that he has given systematic recognition to any differences he found. The classification proposed here is basically synthetic with a stressing of similarities rather than differences although, obviously analysis must precede such a process.

The superfamily contains three morphologically distinct groups which differ in the forms of the lips, of the oesophagus and of the male tail. One is characterized (1) by square lips which are connected by lateral lobes, (2) by a cephalic cap (i.e. a thickening of the cuticle at the anterior end of the body), (3) by a markedly long and narrow oesophagus which expands relatively suddenly into a small posterior trivalvulate oesophageal bulb and (4) by males with relatively long, narrow, evenly pointed tails without alae, typically bearing many small sessile papillae, (5) a relatively small pre-cloacal sucker, (6) having relatively massive, square ended spicules without alae and (7) possessing a gubernaculum. This group I recognize as the Family Aspidoderidae.

The second group is characterized by (1) rounded lips without lateral lobes, (2) no cephalic cap, (3) a relatively short stout oesophagus which merges rather slowly into a relatively large posterior tri-valvulate bulb and (4) by males in which the tail (with the exception of one genus) always carries caudal alae, (5) the spicules are frequently dissimilar and alate, (6) a gubernaculum is generally lacking, and (7) there is a tendency for the pre-cloacal sucker to be prominent and for the caudal papillae to be large. This group I treat as the Family Heterakidae.

The third group is characterized by (1) massive lips without anterior cuticular flanges or (2) lateral lobes or (3) onchia at the anterior ends of the pharyngeal portions which are themselves very small, (4) the oseophagus is grossly club-shaped without a posterior oesophageal bulb or valvular apparatus, (5) the male tail carries the usual circular pre-cloacal sucker with a definite cuticular rim but, although the papillae are grouped round the region posterior to this sucker, they are generally stout and rounded without marked lateral caudal alae, (6) there are frequently files of sessile papillae running down the lateral sides of the body. This group I treat as the Family Ascaridiidae.

I did not previously accept the Family Ascaridiidae as referable to the Heterakoidea (Inglis, 1958; 1958*b*) and argued that it was Ascaridoid. In this I was clearly wrong. I have now studied the Ascaridoidea (Inglis, 1965, 1965*a*) and am convinced by the overwhelming weight of evidence that the Ascaridiidae are heterakoids and that their resemblances to the Ascaridoidea are simply due to the convergent development of a massive body size. The form of the male tail and the presence of paired nuclei in the ventral oesophageal glands are clear features of resemblance with the Heterakoidea and rule against ascaridoid affinities, as does the life history. Equally significant is the structure of the head which in the Ascaridiidae is heterakoid in plan and shows no point of resemblance with that in the Ascaridoidea, other than gross size. The lips in the Ascaridoidea are operated by a septum of three systems of non-contractile fibres (Inglis, 1965) and the cheilorhabdion (i.e. the cuticle lining the inner surface of the cheilostome: Inglis, 1966, 1967) is never markedly sclerotized. In Ascaridiidae the conditions are quite different. The cheilorhabdion is modified into a definite heavily sclerotized region in each lip while the fibre system, which is present, is not organized as three subsiduary systems but is sparse except in the inter-labial regions from which it fans out into each contiguous lip. Exactly the same occurs in the heterakids and aspidoderids. Further the arcade system and associated cells bears no resemblance to that of the Ascaridoidea (Hartwich, 1957).

I continue to treat the Aspidoderidae as a distinct family in spite of Chabaud (1957; 1965) who considers it a subfamily of the Heterakidae. I did at one time agree with Chabaud over this point but further consideration leads me to conclude that to do this masks the many and manifest differences between the aspidoderids and the heterakids. The forms included within the Aspidoderidae differ in so many features from those referred to the Heterakidae, they form such a specialized, geographically restricted group and reach such a degree of independent specialization in a form such as *Lauroia*, that I look on them as being as distinct from the Heterakidae as are the Ascaridiidae.

Lauroia is a particularly aberrant genus at first sight and this has led to its being referred to a unique family within a different Superfamily by Skrjabin *et al.* (1961) but I have studied some of the syntype series of *L. travassosi* Proença, 1938 (type species of the genus) and *L. intermedia* Caballero, 1955. The lips have the interconnecting lobes typical of the aspidoderids and this may be considered a specialized form of the head found in *Paraspidodera*. Further the reduction in the structures of the male tail is so obviously secondary, and has involved all structures, that little stress can be laid on this alone. But in *L. trinidadensis* Cameron, 1939 there is a definite small bump anterior to the pre-cloacal opening which can be considered to be the reduced remnants of a pre-cloacal sucker while the pre-cloacal modification in *L. intermedia* is even more obviously sucker-like.

Family **HETERAKIDAE**

The family Heterakidae, as defined here, contains three distinct morphological groups. The first is characterized by (1) a short, rather stout oesophagus, (2) rather large lips, (3) interlabia (or at least structures which may be interpreted as homologous with inter-labia), (4) a rather large pre-cloacal sucker, and (5) very broad caudal alae supported by long, narrow papillae. The second is characterized by (1) rather small lips which are not set-off from the body, (2) by a relatively small pre-cloacal sucker, (3) by a flap over the vulvar opening, (4) an excretory pore which leads into a lobulate excretory vesicle and (5) by rather narrow caudal alae on the male tail which are supported by three rather small fleshy papillae. The third group is much less homogenous than the others but is characterized by (1) relatively small lips (although the anterior cuticular flange may be large) which are clearly off-set from the remainder of the body by distinct shoulders, (2) by prominent lateral lines, (3) no trace of inter-labia, (4) a relatively long, and narrow oesophagus, and (5) spicules which are always identical and relatively simple in structure. The structure of the male tail is more variable and will be discussed more fully below.

These three groups are treated as subfamilies, thus: (1) Heterakinae, (2) Meteterakinae and (3) Spinicaudinae.

Family **ASPIDODERIDAE**

The family Aspidoderidae consists of two distinct groups in one of which there are inter-labia modified as cordons while in the other there is no trace of inter-labia or cordons.

These two groups are treated as subfamilies: Aspidoderinae and Lauroiinae respectively.

Family **ASCARIDIIDAE**

The family Ascaridiidae contains only one genus, *Ascaridia*.

These taxa are diagnosed formally later.

MORPHOLOGICAL AND EVOLUTIONARY TRENDS

Species of the superfamily occur in all vertebrate groups from amphibia to birds with a few representatives in mammals, except in South American where the Family Aspidoderidae is restricted to Mammals (marsupials, edentates and histricomorph rodents). In view of the great overall similarities between the component taxa it appears reasonable to consider that the superfamily represents a mono-phyletic group.

Within the family Heterakidae there is a sequence along which is a tendency towards a reduction in the number of caudal papillae, with an increase in their size and the associated appearance and increase in the size of the caudal alae. Concomitantly there is a reduction and finally a loss of the gubernaculum, an increase in the relative complexity of the spicules, an increase in the relative size of the pre-cloacal sucker and a loss of papillae on the general body surface with the development of wide lateral alae. There is also a tendency towards the development of cephalic cordons, by the modification of inter-labia associated with the lips, or by the modification of the lips alone.

That these trends have developed in the order described is supported by the host distribution of the parasites. The genera *Spinicauda*, *Africana* and *Meteterakis*, all of which are characterized by papillae on the general surface, relatively large numbers of caudal papillae, a gubernaculum or gubernacular mass, poorly developed caudal alae (when such alae are present), a relatively small pre-cloacal sucker, equal and identical spicules and no interlabia, are restricted to reptiles and amphibia.

The genera *Heterakis*, *Pseudaspidodera* and *Odonototerakis*, on the other hand, are characterized by no papillae on the body surface, relatively small numbers of elongate caudal papillae, no gubernaculum or gubernacular mass, well developed caudal alae, a relatively large pre-cloacal sucker, spicules which are frequently unequal and dissimilar and almost invariably complex, with inter-labia modified as cordons in *Pseudaspidodera* and *Odontoterakis* and are restricted, typically, to birds. Independently the genus *Gireterakis* has developed straight cordons, has no papillae on the general body surface, has very elaborate spicules and is known only from the mammal genus *Hystrix*.

It is now possible to suggest that the form ancestral to the superfamily possessed most of the following characters, although not necessarily all, (1) an anterior cuticular flange which did not project anterior to the mass of the lips; (2) no interlabia; (3) papillae on the general body surface; (4) a relatively long oesophagus with a small posterior oesophageal bulb; (5) a relatively small pre-cloacal sucker on the male tail; (6) no caudal alae on the male tail; (7) equal and identical spicules; (8) many small, sessile caudal papillae on a long, narrow male tail.

The genus *Spinicauda* possesses a combination of characters almost identical with those postulated above for an ancestral form, diverging only in that the anterior cuticular flange of the lips projects slightly anterior to the main mass of the lips, and may be considered as containing the most primitive species of the superfamily (i.e. the most generalized). Non morphological supporting evidence is given by its world-wide occurrance within tropical and subtropical regions and its restriction to reptiles. The characters of the male tail are almost identical with those postulated for an ancestral form and as it is in just those characters that *Spinicauda* resembles the Aspidoderidae I consider the form of the male tail in that family to be relatively unspecialized.

The structure of the head in *Spinicauda* fits into an almost perfect series of increasing elaboration with *Africana*, in which the anterior cuticular flange is wholly within the limits of the lips, *Spinicauda* in which the flanges projects slightly anterior to the main mass of the lips and *Strongyluris* where the flange forms the major part of the lips and dominates the lip-mass completely (Inglis, 1957). It may be pointed out that *Africana* is a close rival to *Spinicauda* for the position of the most primitive genus and may be so considered without affecting the argument presented here.

The connection between the genera *Spinicauda* and *Strongyluris* is accentuated by the forms referred to the genus *Moaciria* (formerly treated as a subgenus of *Spinicauda*). In this latter genus the male tail is intermediate in form between the long narrow tail of *Spinicauda* and the truncate tail, with broad alae, of *Strongyluris*. This transitional form of the male tail is associated with a head which is identical in structure with that of *Spinicauda*.

The genus *Africana* appears to be atypical in being the only genus of the superfamily in which the caudal alae are not supported by caudal papillae, although this could be interpreted as an intermediate stage between the forms without alae and those with alae supported by papillae. The similarities between *Spinicauda*, *Africana*, *Moaciria* and *Strongyluris* are so great and, in addition, can be arranged in such a distinct morphological sequence with fairly clear intermediates culminating in the specialized form of *Strongyluris* that they are treated as a second evolutionary sequence recognized as the subfamily Spinicaudinae.

The remainder of the family Heterakidae falls into two distinct groups, recognized as subfamilies, Heterakinae and Meteterakinae, of which the latter appears to be the result of radiation within a restricted geographical area. The species referred to *Meteterakis* may be considered more primitive than that in *Gireterakis* in possessing a gubernacular mass and in having papillae in the general body surface. *M. triaculeatus* without a gubernacular mass being to that extent intermediate between the two genera.

The subfamily Heterakinae contains the species which are parasitic in birds and are the most highly evolved parasites, morphologically, within the family. Representatives of the subfamily occur in ground feeding, grain-eating birds throughout the world but have become sufficiently distinct in two geographical regions to warrant the recognition of two genera, *Odontoterakis* in South American tinamous and *Pseudaspidodera* in Indian peafowls. The inclusion of *Pseudaspidodera* within the Family Aspidoderidae by Skrjabin *et al.* 1961 is completely unacceptable since not only does it differ from the typical aspidoderids in the structure of the head (Inglis, 1957) but also differs in the form of the male tail with its broad, typically heterakid caudal alae, and the form of the dissimilar spicules. The resemblance must in fact be dismissed as the crudest and most superficial convergence of one morphological feature and if *Pseudaspidodera* is grouped with the aspidoderids so must the genus *Odontoterakis*, which Skrjabin *et al.* do not do.

It is also worth noting that the species referred to the genus *Heterakis* fall into two groups characterized by the structure of the spicules. The groups are not those in which the spicules are equal or unequal (as recognized by many authors, López-Néyra (1947), Skrjabin & Schikhobalova (1947), Freitas (1956) and most recently Skrjabin *et al.* (1961)), but are based on whether the spicules are identical in gross structure although they can be of different lengths (e.i. non-alate without elaborate tips) or are dissimilar (i.e. one, the left, usually bears broad alae and has an elaborate tip while the right is simple and needle-like). This difference is also geographic since the first group is most frequent in the Americas while the other is most characteristic of the European and Asiatic parasites. This difference is also reflected by the structure of the spicules in the neotropical genus *Odontoterakis*, in which the spicules are never alate and never have elaborate tips. The oriental genus *Pseudaspidodera* in contrast is characterized by dissimilar spicules in which the left spicule bears broad alae while the right is needle-like.

The family Aspidoderidae represents the radiation of a stock isolated in South American mammals. In this group most of the diversity is confined to the anterior end of the body, and superficially parallels the conditions in *Pseudaspidodera* and *Odontoterakis* but there are marked differences in the details. Thus, in the heterakids the cordons, when present, never remain the same width throughout their length even when they anastomose (accepting that they do anastomose in *Pseudaspidodera spinosa*, see below). In the family Aspidoderidae the cordons always remain the same width along their full length.

The Aspidoderidae appear to have divided into two lines: one in which inter-labia modified as cordons are present and one in which inter-labia have not appeared. Whether the species referred to *Lauroia* have been derived from the forms grouped in *Paraspidodera* is an open question but in view of the similarities of the head structures the two genera are classified in the same subfamily, Lauroiinae.

The genus *Ascaridia* is clearly heterakoid in affinity but appears to represent a group which diverged fairly early and probably shows its greatest affinities to the Spinicaudinae.

GEOGRAPHICAL AND HOST DISTRIBUTION

The superfamily as a whole is cosmopolitan in distribution and occurs in all vertebrate hosts groups from amphibia to mammals and birds, but it is in the latter group that it is most frequent and wide-spread. The distribution of the major subdivisions of the superfamily is interesting since it reflects a combination of host and geographical restrictions. Thus, the subfamily Spinicaudinae is cosmopolitan with forms occurring in all major geographical regions although restricted to reptiles and amphibia. Even the genera within the subfamily tend to be wide-spread. *Spinicauda* occurs in South America, Africa, Madagascar and Australia, with one species in each area, while *Strongyluris* is extremely widely spread in tropical and subtropical regions and is represented by a much larger number of species. In contrast *Africana* is restricted to Africa, and *Moaciria* to South America, Africa and Madagascar. *Strongyluris* appears to represent the culmination of the Spinicaudinae and is as successful as a group of parasites in reptiles as the genus *Heterakis* is in birds.

The subfamily Heterakinae is equally wide-spread but is largely restricted to ground-feeding, grain-eating birds i.e. Galliformes (one species in mammals; *H. spalacis* and *H. macrospiculum* are not typical of the genus *Heterakis* and are best considered *incertae sedis* although the latter shows similarities to *Africana*, particularly in the structure of the male tail and spicules.) The genus *Heterakis* is cosmopolitan and ubiquitous but the other genera of the subfamily are geographically restricted with *Odontoterakis* in South America and *Pseudaspidodera* in the Indian region.

The family Aspidoderidae is the only group of the superfamily which occurs widely in mammals and it also is geographically restricted to South America while *Ascaridia*, although cosmopolitan, is most commonly reported from members of the Columbiformes and Psittaciformes although it is not uncommon in the Galliformes.

The patterns suggest that the evolution of the superfamily has been due to a combination of (1) intra-host restriction to the caecum, (2) host restriction to ground-feeding grain-eating birds and (3) geographical restriction. There is no evidence to suggest any close host : parasite parallelism. The impression is rather of a group which has evolved and expanded to occupy all the space available to it within the constrains of the ecology and feeding habits of the hosts (see Inglis, 1965b).

Thus the members of the superfamily exist in a specialized, selected, locality within the host, in all birds in which they occur. But they only occur in a restricted range of hosts with similar feeding habits. Then the various smaller taxa are largely determined geographically. Nevertheless the Aspidoderidae represent a special case in that they are not only geographically isolated but also occur in a long isolated group of mammalian hosts, the South American marsupials and the ground-feeding edentates. It should be noted that they do not occur in the ant-eaters or the tree-dwelling sloths. It is interesting to wonder, although impossible to know, if they *continue* to exist in South America because there is no competition with other nematode parasites in the large intestine where they occur or whether they represent a new group of parasites which has replaced some other group. In other words are they a remnant group or are they the result of a specialized radiation within an isolated geographical and host locality?

Be that as it may the Heterakoidea is clearly an old group which is supremely successful within the hosts groups in which it occurs.

SYSTEMATIC HISTORY

Railliet and Henry (1914) considered that the species of the family Ascaridae for which they had created a new subfamily Heterakinae in 1912 were sufficiently distinct to warrant their further separation into a distinct family, Heterakidae. This family was diagnosed largely on the presence of a pre-cloacal sucker on the male tail and included the genera *Heterakis*, *Ascaridia*, *Aspidodera*, *Cissophylus* and *Subulura*, with *Strongyluris* as a subgenus of *Heterakis* and *Oxynema* as a subgenus of *Subulura*. No groupings higher than genera were proposed.

Travassos (1920) introduced two new genera, *Spinicauda* and *Africana*, and later in the same year (Travassos, 1920*a*) he divided the family Heterakidae into three subfamilies: Heterakinae, with *Heterakis*, *Ganguleterakis*, *Aspidodera*, *Paraspidodera* and *Gireterakis*; Spinicaudinae nov. for *Spinicauda*, *Africana* and *Strongyluris*; Subulurinae for *Subulura*, *Heteroxynema*, *Oxynema* and *Numidica*. The last subfamily differed from both the others in having in the males an elongate pre-cloacal sucker without a definite rim while the other two had a pre-cloacal sucker with a definite cuticular rim. The diagnostic differences between the other two subfamilies were vague and appear to have been mainly the restriction of the species of the first to warm-blooded hosts and those of the second to cold-blooded hosts.

Yorke & Maplestone (1926) considered the subfamily Subulurinae a family and did not recognize the subfamily Spinicaudinae, thus leaving the family Heterakidae with no groups higher than genera. Baylis & Daubney, slightly later in the same year (1926), still treated the subulurids as a subfamily but this was not generally accepted.

No further radical changes were proposed in the classification of the Heterakidae until Skrjabin and Schikhobalova (1947) recognized two subfamilies: Heterakinae and Aspidoderinae nov. This grouping was largely based on published descriptions and the subfamilies were considered distinct almost wholly on the presence or absence of cephalic cordons. In 1957 I described the comparative anatomy of the head in the family and argued that the classification of Skrjabin and Schikhobalova was unnatural because cephalic cordons appeared to have been developed independently three times. I then proposed that the genera *Aspidodera*, *Ansiruptodera*, *Sexansodera* and *Paraspidodera* be placed in a separate family, Aspidoderidae with two subfamilies: Aspidoderinae for the first three of the above genera and Paraspidoderinae nov. for the fourth.

Independently Freitas (1956) reviewed the family and proposed four new families, four new subfamilies and five new genera (four with one species each and one with two species). This classification was, and still is, unacceptable. There are five families of which two have only one species, there are eight subfamilies of which three have only one genus each, there are twenty-two genera of which eleven have only one species each and four have only two species each. This classification was based largely on published descriptions and every error of observation and every faulty description appears to have been recognized by a distinct genus, at least, and in some cases a subfamily or even family.

Then Chabaud (1957), in considering the classification of the suborder Ascaridina introduced a new superfamily Heterakoidea which he considered to contain two families and four subfamilies thus: Heterakidae, with four subfamilies Heterakinae (with sixteen genera or subgenera), Aspidoderinae (with four genera or subgenera), Lauroiinae (with one genus) and Schneidernematinae (with one genus); and the family Ascaridiidae with one genus, *Ascaridia*. This classification is largely that of Inglis (1957) and Freitas (1956) re-arranged.

In 1958 I proposed the classification which I am justifying here and will not discuss it now accept to draw attention to the fact that *Schneidernema* and *Morgascaridia* (a genus I proposed for *Paraspidodera sellsi*, Morgan, 1928: Inglis, 1958*b*) were removed from the Heterakidae first to the Ascaridiidae (Inglis, 1958*b*) and later to the Superfamily Seuratoidea (Inglis & Chabaud, 1958) as members of a distinct subfamily Schneidernematinae.

Most recently Skrjabin, Schikhobalova & Lagodovskaja (1961) have presented a re-arrangement of the Heterakoidea, with four families, thus : Heterakidae : Heterakinae (*Heterakis*, *Ganguleterakis* and *Odontoterakis*); Meteterakinae (*Meteterakis*; and *Gireterakis*).

Aspidoderidae : Aspidoderinae (*Aspidodera*, *Ansiruptodera* and *Sexansodera*) Spinaspidoderinae (*Spinaspidodera* and *Pseudaspidodera*).

Spinicaudidae : Spinicaudinae (*Spinicauda*, *Africana* and *Paraspidodera*) ; Preterakinae (*Preterakis*).

Strongyluridae : Strongylurinae (*Strongyluris* and *Moaciria*).

In addition they refer *Lauroia* to a distinct family within the Cosmocercoidea and introduce a new genus, *Bellaplectana* for *Aplectana pharyngeodentata* Belle, 1957.

It should, perhaps, be pointed out that Yamaguti (1961) has grouped the Heterakoidea in yet another way but this does not warrant serious consideration except to dismiss the new genus *Cheloniheterakis*. This genus was introduced for two old and inadequately described species from *Testudo*. No other heterakids are known from this host genus in which members of the family Kathlaniidae are fairly common parasites. As the two species referred to *Cheloniheterakis* possess circular precloacal suckers, which are common in Kathlaniids it is more probable they are referable to that family. Be that as it may the two species are *species dubia* and the genus must be ignored as unrecognizable.

The Skrjabin *et al.* classification does warrant consideration and I will give my arguments against accepting it. Part of it can be dismissed quickly and easily as due to classifying errors of description. The arguments against the genus *Bellaplectana* have been adumbrated at the beginning of this paper but to recapitulate briefly the so-called teeth in the head, upon which the genus is based, do not exist they are simply the retracted lips in poorly fixed specimens. The genus *Preterakis* and the associated subfamily Preterakinae must disappear since the fusion of the caudal alae on the ventral surface of the male body is a fixation artefact and does not occur in all the specimens of the type series. The remaining arguments are more expressions of opinion and of assessing the weight of the morphological and other evidence, thus :

The reference of the aspidoderids and *Pseudaspidodera* to the same family is a continuation of the position taken by Skrjabin & Schikhobalova (1947) but is still un-acceptable and morphologically indefensable. If this grouping is advocated there is no real reason for not referring *Odontoterakis* to the same family, but this genus is referred by Skrjabin *et al.* (1961) to the Heterakidae. I stress, and repeat what I wrote before, the only resemblance between the Aspidoderidae and *Pseudaspidodera* is in the common possession of structures called by the same name, i.e. cordons. The family Aspidoderidae (sensu Skrjabin *et al.*) is otherwise characterized (in addition to cordons) by the presence of a cephalic cap, inter-connecting lobes to the lips, a long slim oesophagus and, in the male, is further characterized by equal and identical square-ended spicules, no caudal alae and the presence of many sessile papillae. In all these respects *Pseudaspidodera* differs from the Aspidoderids and in all the corresponding features is identical with the genera referred by Skrjabin *et al.* to the subfamily Heterakinae.

Equally the reference of *Paraspidodera* to the Spinicaudinae is unacceptable since its only resemblance to the other genera of that subfamily is in lacking caudal alae and cephalic cordons. In all other respects, the structure of the head, the oesophagus, and the male's tail and spicules it is indistinguishable from the forms referred to the Aspidoderidae. The reference of *Lauroia* to the superfamily Cosmocercoidea is equally contradicted by the morphology. The structure of the anterior end of the body is very similar to that of the Aspidoderidae and the remnants of a pre-cloacal sucker are clearly present in at least two species.

The separation of *Strongyluris* and *Moaciria* (which I now accept as a distinct genus) into a separate family is equally unacceptable since *Strongyluris* so clearly represents the end of a morphological sequence running from *Spinicauda* to *Moaciria* to *Strongyluris*. The structure of the head in *Moaciria* is identical with that in *Spinicauda* while the male tail forms an almost perfect intermediate between that genus and *Strongyluris*.

I therefore propose the following classification for the Superfamily Heterakoidea.

ANNOTATED CLASSIFICATION OF THE SUPERFAMILY

On the basis of the arguments presented above the following classification is proposed. Notes are appendaged to each group to draw attention to points of interest and to explain some of the names used. In these notes some of the argument given above is briefly repeated so that this section is more or less complete in itself.

HETERAKOIDEA (Ralliet & Henry, 1912) Chabaud, 1957

Ascaridida : three large distinct lips, one dorsal with two double papillae, two ventral with a double ventral papilla and a single lateral papilla each : lining of mouth cavity (i.e. cheilorhabdion) sclerotized and forming a flange along the anterior edge of each lip in all forms except *Ascaridia* ; anterior end of oesophagus divided into three projecting lobes, one to each lip, except in *Ascaridia* ; nuclei of ventral oesophageal glands double ; no intestinal or oesophageal appendices.

MALE : circular pre-cloacal sucker with a definite cuticular rim ; two spicules.

FEMALE : eggs not embryonate *in utero*, thick-shelled ; vulva opening about middle of body.

LIFE HISTORY : Direct, with or without a migration within the final host.

HOSTS : Restricted to the intestine (more specifically to the caecum in birds and the large intestine in mammals) of ground feeding birds and mammals. In amphibia (anurans) and reptiles (saurians) restricted to terrestrial feeders.

GEOGRAPHICAL DISTRIBUTION : Cosmopolitan as a superfamily.

HETERAKIDAE Railliet & Henry, 1912

Heterakoidea : lips rounded, not connected by lateral lobes ; cordons when present poorly developed and not remaining the same width throughout their length ; oesophagus relatively short and stout.

MALES : caudal alae typically present ; number of caudal papillae relatively low ; spicules may be unequal and dissimilar ; gubernaculum generally reduced or absent ; tail generally relatively short.

HOSTS : amphibia, reptiles and (mainly) birds. One species in mammals.

DISTRIBUTION : Cosmopolitan as a family.

TYPE GENUS : *Heterakis* Dujardin, 1845.

HETERAKINAE Railliet & Henry, 1912

Heterakidae : lips not off-set from body ; anterior cuticular flange of lips generally not projecting beyond main lip mass ; inter-labia, or their homologues, present.

MALE : precloacal sucker relatively large ; caudal alae broad, supported by long, narrow papillae ; gubernaculum lacking ; spicules frequently dissimilar.

HOSTS : mainly birds, one exceptional species in mammals (rodents).

DISTRIBUTION : Cosmopolitan.

The subfamily is a homogeneous group in which three subgroups can be recognized. *Odontoterakis* is South America, *Pseudaspidodera* in India and *Heterakis* which is cosmopolitan. The latter genus is characterized by lacking definite cephalic cordons such as characterize the other two genera. But there is a tendency for there to be marked " bumps " in the inter-labial spaces which may be considered as precursors of the inter-labia which are modified as cordons in the other two genera. It is worth pointing out that what are here called cordons are identical in form and origin with the so-called labial grooves of some members of the Ascaridoidea, e.g. *Porrocaecum* and *Multicaecum*. These labial grooves are also formed from two sources, one the inter-labia and the other the lips, and also consist of open grooves.

The morphological differences between *Pseudaspidodera* and *Odontoterakis* tend to be slight but in the former genus, in addition to the cordons being more strongly developed, the left spicule is always shorter than the right, is always broadly alate while the right is slim and needle-like, and generally has an elaborate posterior tip. In contrast the spicules in *Odontoterakis* are always identical in structure, never bear alae, and always end posteriorly in simple points.

I therefore interpret the two groups as having developed in specialized host groups within isolated geographical areas since *Pseudaspidodera* appears to have arisen in peafowls in India and *Odontoterakis* to have arisen in tinamous in South America. Both host groups being typically ground dwelling forms with poor powers of locomotion.

Heterakis Dujardin, 1845

Heterakinae : lips without definite inter-labia or cordons.

MALES : spicules frequently dissimilar but may be equal and identical.

TYPE SPECIES : *Ascaris gallinarum* Schrank, 1788.

HOST AND GEOGRAPHICAL DISTRIBUTION : ground feeding birds, mainly Galliformes, throughout the world.

Several attempts have been made to divide this genus into two on the basis of the relative lengths of the spicules, species with equal spicules to one genus and with unequal to another. Both López-Néyra (1947) and Skrjabin & Schikhobalova (1947*a*) independently attempted to do this, using the name *Ganguleterakis* for species with equal spicules. Madsen (1950), in a generally excellent and outstanding publication, commented upon this unfavourably pointing out the great difficulty in many cases in deciding whether the spicules should be called equal or unequal. Freitas (1956) attempted to over-come this difficulty by defining his two subgenera, *Heterakis* and *Raillietakis*, so that unequal spicules were considered to be those in which the difference in length was at least one third the length of the shorter spicules. Even with this qualification it is difficult to imagine that equality or its lack is a sufficiently fundamental character upon which to recognize genera or subgenera.

Skrjabin *et al.* (1961) continue to recognize two groups on just this difference in the lengths of the spicules but it is still unacceptable. It is so very clearly a bibliographical key character resorted to in an attempt to reduce the number of species within each genus and can only have been used because it is one of the few characters which can be determined from literature rather than specimens.

The structure and relative lengths of the spicules, nevertheless afford good characters in the delimitation of species within the genus used in conjunction with the number of caudal papillae, the relative size and position of the pre-cloacal sucker and the relative length of the male tail. Many authors have laid stress on the position of various caudal papillae, e.g. the number of pre-cloacal papillae, but as Maplestone (1932) and Madsen (1950), among others, have pointed out, the value of these characters is very limited.

The typical arrangement of the caudal papillae is described above but it should be noted that it is relatively common for an additional pair to occur between the para-cloaca and suctorial groups or for one of the pairs of para-cloacals to be missing. There is also a tendency, in the species occurring in South America, for a pair of long papillae to be present just anterior to the peri-cloacal group, a pair which I consider homologous with the anterior pair of peri-cloacals since in specimens on which the former pair of papillae are present the latter pair is consistently absent.

Both Maplestone (1932) and Madsen (1950) have pointed out that it is, in most cases, impossible to find characters by which the females of *Heterakis* may be distinguished. This applies throughout the entire superfamily. I have been unable to find any character, or combination of characters by which females alone can be identified.

In spite of my criticism of the attempts to divide the genus *Heterakis* on the basis of the relative lengths of the spicules two subgroups can be recognized: (1) one in which the spicules are identical in structure and never bear alae and (2) one in which the spicules are dissimilar with the right slim and needle-like and the left broadly alate. In this latter group the posterior end of the left spicule is frequently modified into a hook or barb. In both groups the spicules may be unequal in length but in the first group when there is any modification on the posterior end it is always identical in both spicules. Thus on this basis *H. gallinarum* and *H. isolonche*, which only differ in the relative lengths of the spicules, fall together while on the basis of unequality they are completely separated.

Lane (1914) introduced the generic name *Ganguleterakis* for the species generally known as *H. spumosa* Schneider, 1866. There is a case for recognizing this genus as it contains the only species of *Heterakis* from mammals (*H. spalacis* and *H. longispiculum incertae sedis*) but, except for a reduction in the number of caudal papillae, in which it is paralleled by *H. psophiae* Travassos, 1913, it is a typical *Heterakis*. I do not, therefore, recognize this genus.

Odontoterakis Skrjabin & Schikhobalova, 1947*a*

Heterakinae: interlabia modified as non-recurrent cordons.

MALES: spicules simple non-alate and identical in structure.

TYPE SPECIES: *Heterakis crypturi* Baylis, 1944.

HOST AND GEOGRAPHICAL DISTRIBUTION: Birds, mainly tinamous, in South America.

Note: A restudy of the types of *Heterakis interlabiata* Ortlepp, 1923 has convinced me that Mendonça (1953) is correct in treating it as a synonym of *H. isolonche*.

Pseudaspidodera Baylis & Daubney, 1922

Heterakinae: inter-labia modified as recurrent cordons.

MALES: spicules dissimilar and unequal, right slim and needle-like, left with broad alae.

TYPE SPECIES: *Pseudaspidodera pavonis* Baylis & Daubney, 1922.

HOST and GEOGRAPHICAL DISTRIBUTION: Phasianid birds, India.

P. jnanendrae Chakravarty, 1938 was described as having anastomosing cordons but in the type, a female, the head is very contracted and it is probable that the apparent fusion is an artefact. *P. spinosa* Maplestone, 1932 was described as having spines in the cordons which anastomose. As a result a genus *Spinaspidodera* was proposed by Skrjabin & Schikhobalova (1947) for it. There is some justification for this but in view of the small number of species involved and as Maplestone's species has never been rediscovered and the types are lost I prefer not to recognize this genus. It is worth noting that the cordons in this case, if they do definitely anastomose, vary in width along their length and do not remain the same width as in the members of the Aspidoderidae.

METETERAKINAE Inglis, 1958*a*

Heterakidae : head with three rounded lips, without interlabia ; oesophagus relatively long with a small postoesophageal bulb ; excretory pore opening into a large lobulate vesicle ; lateral alae running full length of body.

MALE : spicules equal in length ; caudal alae present, supported by three pairs, exceptionally four, of large fleshy papillae—one pair lateral to the cloacal opening and typically two pairs, exceptionally three, lateral to the small pre-cloacal sucker ; a large number generally about twenty pairs, of small sessile papillae also present.

FEMALE : vulvar opening covered by a flap developed from the anterior lip ; tail relatively very long.

TYPE GENUS : *Meteterakis* Karve, 1930.

HOST AND GEOGRAPHICAL DISTRIBUTION : Amphibia, reptiles and mammals (*Hystrix*) in the oriental region (s.l. : India, Ceylon, China, Japan, East Indies, Burma).

Meteterakis Karve, 1930

Meteterakinae : head without cordons ; body generally with many small sessile papillae scattered over surface.

MALES : spicules identical ; indefinite gubernacular mass developed from the walls of the cloaca—except in *M. triaculeata* ; posterior lip of cloacal opening covered by small granulations.

TYPE SPECIES : *Meteterakis govindi* Karve, 1930.

HOST AND GEOGRAPHICAL DISTRIBUTION : amphibia and reptiles, as for subfamily.

Gireterakis Lane, 1917

Meteterakinae : anterior cuticular flange of lips not projecting anterior to main lip mass ; three straight, simple cordons, one arising from each inter-labial space.

MALE : number of sessile caudal papillae relatively small ; spicules elaborate ; no gubernacular mass present.

TYPE SPECIES : *Gireterakis girardi* Lane, 1917.

HOST AND GEOGRAPHICAL DISTRIBUTION : *Hystrix* species in India.

SPINICAUDINAE Travassos, 1920

Heterakidae : lips off-set from body ; no inter-labia or cordons ; lateral fields prominent ; papillae on body.

MALE : spicules equal, identical and simple ; papillae do not support caudal alae when alae present except when the tail is short and the pre-cloacal sucker is directed posteriorly.

TYPE GENUS : *Spinicauda* Travassos, 1920.

HOST AND GEOGRAPHICAL DISTRIBUTION : Amphibia and reptiles ; cosmopolitan in the tropics and sub-tropics.

This subfamily is morphologically the least uniform, and therefore the most difficult to diagnoze, in the superfamily Heterakoidea. This is mainly because *Spinicauda* is morphologically generalized while *Strongyluris* is highly modified. A trend in the modification of the head is apparent from *Africana*, with a simple anterior cuticular flange, to *Spinicauda* and *Moaciria* in which the flange projects slightly beyond the lip mass to *Strongyluris* in which the flange forms the major part of the lip. *Moaciria* forms an almost perfect intermediate stage between *Spinicauda* and *Strongyluris* since it resembles *Spinicauda* in the presence of a gubernaculum and in having the same head form and resembles *Strongyluris* in the posteriorly directed pre-cloacal sucker and the presence of caudal alae (narrow) supported by longish papillae. I treated *Moaciria* as a subgenus of *Spinicauda* in 1958 but now prefer to treat it as a distinct genus.

Spinicauda Travassos, 1920*a*

Spinicaudinae : anterior cuticular flange projects slightly beyond the main mass of the lips.

MALE : tail relatively long, tapering evenly to a point ; pre-cloacal sucker relatively small ; gubernaculum present ; caudal papillae small and sessile.

TYPE SPECIES : *Ascaris spinicauda* Rudolphi, 1819.

HOST AND GEOGRAPHICAL DISTRIBUTION : Reptiles in South America, Africa, Madagascar and Australia (Queensland). i.e. tropical and subtropical.

Africana Travassos, 1920

Spinicaudinae : anterior cuticular flange not projecting anterior to lips ; lateral alae present.

MALES : pre-cloacal sucker small ; spicules equal and identical, alate ; gubernacular mass present ; small sessile papillae on tail ; caudal alae not supported by papillae ; caudal alae stop about level of cloacal opening.

TYPE SPECIES : *Heterakis africana* Gendre, 1909.

HOST AND GEOGRAPHICAL DISTRIBUTION : Amphibia and reptiles in tropical and subtropical Africa.

Moaciria Freitas, 1956*a*

Spinicaudinae : anterior cuticular flange projecting slightly anterior to mass of lips.

MALE : tail relatively long with relatively few stoutish papillae supporting narrow caudal alae ; posteriorly directed pre-cloacal sucker ; gubernaculum present.

TYPE SPECIES : *Moaciria alvarengai* Freitas, 1956*a*.

HOST AND GEOGRAPHICAL DISTRIBUTION : Reptiles in South America, Africa and Madagascar.

Strongyluris Mueller, 1894

Spinicaudinae : anterior cuticular flange projecting beyond main lip mass so that it forms major portion of lip ; sessile papillae scattered over body surface.

MALE : posterior end obliquely truncate ; pre-cloacal sucker relatively large and directed posteriorly ; caudal alae well developed, supported by rather long, stout caudal papillae ; spicules equal, without alae ; no gubernaculum or gubernacular mass present.

TYPE SPECIES : *Strongyluris brevicaudata* Mueller, 1894.

HOST AND GEOGRAPHICAL DISTRIBUTION : Mainly reptiles, rarely amphibians, cosmopolitan within the tropics and subtropics.

ASPIDODERIDAE Skrjabin & Schikhobalova, 1947

Heterakoidea : lips square connected by lateral lobes ; cuticle at anterior end of body thickened to form a cephalic cap ; oesophagus long and narrow with a small posterior oesophageal bulb ; cordons, when present, the same width along their lengths.

MALES : no caudal alae ; gubernaculum generally present ; spicules equal in length and identical in structure, generally massive ; generally many small sessile papillae on long, narrow tail ; caudal papillae all about the same size.

TYPE GENUS : *Aspidodera* Railliet & Henry, 1912.

HOSTS AND GEOGRAPHICAL DISTRIBUTION : Marsupials, edentates and occasionally hystricomorphs in South America and related areas.

ASPIDODERINAE Skrjabin & Schikhobalova, 1947

Aspidoderidae: cephalic cordons present, lateral lobes of lips complex.

TYPE GENUS : *Aspidodera* Railliet & Henry, 1912.

DISTRIBUTION : As family.

Aspidodera Railliet & Henry, 1912

Aspidoderinae : cephalic cordons recurrent and anastomosing.

TYPE SPECIES: *Aspidodera scoleciformes* Diesing, 1851.

Ansiruptodera Skrjabin & Schikhobalova, 1947

Aspidoderinae : cephalic cordons not anastomosing.

TYPE SPECIES : *Aspidodera ansiruptodera* Proença, 1937.

LAUROIINAE Skrjabin & Schikhobalova, 1951

Aspidoderidae : cephalic cordons lacking ; lateral lobes of lips simple.

TYPE GENUS : *Lauroia* Proença, 1938.

HOST AND GEOGRAPHICAL DISTRIBUTION : Edentates and hystricomorphs, as the family.

Lauroia Proença, 1938

Lauroiinae : cephalic cap modified into three " plates " which are slightly undercut posteriorly. This modification can be interpreted as due to the development of cordons which do not involve inter-labia as in *Gireterakis*.

MALE : posterior end simple without a gubernaculum, relatively few papillae, and a reduced pre-cloacal sucker.

TYPE SPECIES : *Lauroia travassosi* Proença, 1938.

Paraspidodera Travassos, 1914

Lauroiinae : cephalic cap not modified as " plates ".

MALE: posterior end relatively complex, with a gubernaculum; relatively large number of caudal papillae and a well developed pre-cloacal sucker.

TYPE SPECIES : *Paraspidodera uncinata* Rudolphi, 1819.

ASCARIDIIDAE Travassos, 1919

Heterakoidea : lips large and stout ; no distinct anterior cuticular flange ; oesophagus club-shaped without a posterior bulb.

MALE : caudal alae narrow supported by short stout papillae.

TYPE GENUS : *Ascaridia* Dujardin, 1845.

HOST AND GEOGRAPHICAL DISTRIBUTION : Birds, cosmopolitan with rare species in mammals.

KEY TO THE GENERA OF THE SUPERFAMILY HETERAKOIDEA

(1) (2) Without a tri-valvulate posterior oesophageal bulb . . . ASCARIDIA (p. 24)
(2) (1) With a tri-valvulate posterior oesophageal bulb . . . . (3)
(3) (18) Head without a cephalic cap, without interconnecting lobes to lips . . (4)
(4) (9) Anterior cuticular flange of lip not projecting anterior to main lip mass, no papillae on body, lateral alae present, broad caudal alae supported by long, thin papillae . . . . (5)
(5) (6) Head without cordons or labial grooves . . . . HETERAKIS (p. 19)
(6) (5) Head with cordons or labial grooves . . . . (7)
(7) (8) Spicules dissimilar, left with broad alae, right needle-like, restricted to India and associated regions. . . . . . . PSEUDASPIDODERA (p. 20)
(8) (7) Spicules similar, never alate, restricted to South America ODONTOTERAKIS (p. 20)
(9) (15) Narrow lateral alae, papillae on body surface, caudal alae when present either not supported by papillae or supported by many short, stoutish papillae . (10)
(10) (11) No caudal alae on male tail . . . . SPINICAUDA (p. 22)
(11) (12) Caudal alae not supported by papillae . . . . AFRICANA (p. 22)
(12) (15) Caudal alae supported by stout papillae, male tail obliquely truncate, and sucker directed posteriorly . . . . (13)

(13) (14) Male tail without long terminal spike, anterior cuticular flange major part of lip . . . . Strongyluris (p. 23)
(14) (13) Male tail with long terminal spike, anterior flange not major part of lip Moaciria (p. 22)
(15) (9) Caudal alae supported by 3–4 stout papillae . . . . . . (16)
(16) (17) Straight cordons running posteriorly from interlabial spaces, spicules very complex . . . . Gireterakis (p. 21)
(17) (16) No cordons, spicules not very complex . . . . Meteterakis (p. 21)
(18) (3) Head with a cephalic cap, interconnecting lobes to lips . . . . (19)
(19) (22) Head without cordons . . . . (20)
(20) (21) Head with three cuticular " plates ", pre-cloacal sucker reduced, or lacking Lauroia (p. 24)
(21) (20) Head without cuticular " plates ", sucker normal . . Paraspidodera (p. 24)
(22) (19) Head with cordons . . . . (23)
(23) (24) Cordons not anastomosing . . . . . . Ansiruptodera (p. 23)
(24) (23) Cordons anastomosing . . . . Aspidodera (p. 23)

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APPENDIX

While this paper was in press Chabaud (Alain G.) and Dollfus (Robert Ph.) have published the description of a new genus and species of heterakid (1966, *Hatterianema hollandei* N.G., N.SP., nematode hétérakide parasite de rhynocéphale. *Bull. Mus. nat. hist. Nat.* Ser. 2, **37** : 1041–1045) which they refer to the subfamily Meteterakinae.

However, from the description the species is referable to the Spinicaudinae rather than Meteterakinae since 1) the lips appear to be offset from the body, 2) there are no caudal alae on the male tail, 3) a gubernaculam is present, 4) there is no flap over the vulva in the female. In the key given above *H. hollandei* comes out at *Spinicauda* from which *Hatterianema* appears to differ largely in not possessing a cuticular flange projecting beyond the main mass of the lips and the large number of caudal papillae. In fact *Hatterianema* corresponds almost perfectly to the hypothetical ancestral form deduced above.

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PART VI

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British Museum (Natural History)

Pp. 29–119; 24 *Text-figures*

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INTRODUCTION

THIS is the second of two papers dealing with the piscivorous species of *Haplochromis* in Lake Victoria. In the first part (Greenwood, 1962) representatives of the principal groups of piscivores were considered, and the main morphological trends within the trophic grade were discussed. The present paper covers the remaining species which have been studied to date ; undoubtedly more piscivorous *Haplochromis* species will be discovered, particularly amongst the as yet poorly sampled species of the deeper waters.

Not every species considered here is a piscivore ; those of other trophic groups are included simply because the species have the morphology of a piscivore, and presumably evolved from the same stem as their fish-eating relatives.

Also included in this paper is a species apparently endemic to the Lake Kyoga system. This step was necessary because of its close relationship with a previously undescribed species from Lake Victoria.

Some of the individual species described below, and in the previous paper, would seem to be so far removed from the generality of Victoria *Haplochromis* species as to justify their elevation to generic rank. Indeed, it could be argued that even some of the species-complexes have attained this level of differentiation. However, I do not think that the question can be dealt with until the whole Lake Victoria *Haplochromis* species-flock has been described. Even then, I doubt whether it will be possible to make any such divisions, at least generically. Perhaps a number of subgeneric groups could be justified on phyletic grounds, but these will be difficult to define. The situation closely resembles that encountered by Trewavas (1964) in the genus *Serranochromis*. However, I do not believe that her solution to the *Serranochromis* problem, the recognition of a gradal genus, is applicable to the situation amongst the piscivorous *Haplochromis* of Lake Victoria, particularly because the boundary between these species and any ancestral grade (or grades) would be even more obscure and indefinite than that separating *Serranochromis* from the *Haplochromis* of central Africa. Further complications are introduced when one considers the generic status of "*Haplochromis*" species outside Lake Victoria (and this includes the Lake Nyasa species in all their complexity) relative to the possibly polygeneric *Haplochromis* species of Lake Victoria.

Haplochromis spekii (Boulenger), 1906

(Text-fig. 1)

Pelmatochromis spekii (part) Boulenger, 1906, *Ann. Mag. nat. Hist.*, (7), **17**, 440; *Idem*, 1915, *Cat. Afr. Fish*, **3**, 416, fig. 285. (Lectotype, B.M. (N.H.), reg. no. 1906.5.30.296, and probably one paralectotype, 1906.5.30.307).

Haplochromis spekii (part): Regan, 1922, *Proc. zool. Soc. Londn.*, 179 (same specimens as above).

Haplochromis serranoides Regan, 1922, *op. cit.* (Lectotype, B.M. (N.H.) 1911.3.27.17, and probably the two paralectotypes 1904.5.19.52–3).

? *Paratilapia serranus* (part): Boulenger, 1915, *Cat. Afr. Fish*, **3**, 334 (two specimens, 1904.5.19.52–3, see above).

? *Haplochromis serranus* (part): Regan, 1922, *op. cit.* 174 (paralectotype of *P. spekii* 1904.5.30.307, see above).

LECTOTYPE: a male, 191·0 mm. S.L., from Bunjako, collected by Degen; B.M. (N.H.) reg. no. 1906.5.30.296.

NOTE ON THE SYNONYMY: Certain small specimens (those indicated above with an interrogation mark) are included in the synonymy with some uncertainty. Using the diagnostic characters currently available, small preserved specimens of *H. spekii* cannot readily be separated from similar sized specimens of *H. serranus*.

Regan (1922) distinguished *H. spekii* from *H. serranoides* on two characters: the maxillary extending to below the anterior quarter of the eye (barely reaches anterior orbital margin in *H. serranoides*), and, the caudal peduncle longer than deep (as long as deep in *H. serranoides*). Additional material shows that the difference in caudal peduncle proportions is easily masked by intraspecific variability; furthermore, I am unable to confirm the marked differences in caudal peduncle proportions which Regan found in the lectotypes of the two species. The difference in the posterior extension of the maxilla is valid for the lectotypes, but it must be noted that the jaws in *H. spekii* type are somewhat distorted because of a deformed right preorbital bone. Again, more material has shown that the maxilla has a variable posterior extension which links the extremes shown by the lectotypes of the two species.

In all other characters, including the dentition and the preserved colour patterns, the two type specimens show no trenchant differences, and I consider them to be conspecific.

Because of their small size (74 and 114 mm. S.L.) the paralectotypes of *H. serranoides* have not been included in the redescription. I think it probable that these specimens are referable to the species. A similar problem is posed by three paralectotypes of *H. spekii* (B.M. [N.H.] reg. nos. 1906.5.30.301, and 1906.5.30.297–8, of standard lengths 101·0, 91·0 and 79·0 mms. respectively). The two latter may perhaps be specimens of *H. serranus*, and the former is probably referable to *H. spekii*. However, until more is known about the characteristics of smaller specimens of *H. spekii*, I consider it inadvisable to give a definite identity to these three fishes.

DESCRIPTION : based on 44 specimens (including the lectotype of the species, and the lectotype of *H. serranoides*), 128–220 mm. standard length.

Depth of body 32·8–39·8 (mean, M = 35·6) per cent of standard length, length of head 36·1–39·3 (M = 37·4) per cent. Dorsal head profile straight, sloping at an angle of 30°–35°, the premaxillary pedicels from barely to moderately prominent and interrupting the profile.

Preorbital depth 18·0–24·2 (M = 20·7) per cent of head, least interorbital width 22·0–26·0 (M = 23·3) per cent. Snout 1·2–1·3 times as long as broad, its length in fishes $<$ 190 mm. S.L., (N = 25), 34·0–40·6 (M = 36·8) per cent of head, and in larger fishes (N = 19) 36·0–42·5 (M = 39·1) per cent. Eye diameter in fishes $<$ 200 mm. S.L. (N = 34) 17·3–22·6 (M = 20·0), and in larger individuals (N = 10) 15·7–19·4 (M = 18·0) per cent of head; ratio of eye/preorbital 0·8–1·3 (M = 1·0). Depth of cheek 25·7–32·9 (M = 29·5) per cent of head.

Caudal peduncle 16·7–19·8 (M = 17·9) per cent of standard length, 1·1–1·5 (modal range 1·2–1·3) times as long as deep.

Mouth horizontal or slightly oblique, jaws equal anteriorly or the lower projecting slightly, its length 49·2–61·3 (M = 53·8) per cent of head, 1·7–2·6 (modal range 1·9–2·1) times as long as broad. Mental symphysis smooth or with a slight protuberance. Premaxilla sometimes a little expanded medially but never beaked. Posterior tip of the maxilla reaching a point near the vertical through the anterior orbital margin or occasionally reaching this level (see also note on synonymy, p. 32).

Gill rakers: stout or moderately stout, the lower 1 to 3 reduced; 8 or 9 (rarely) on the lower part of the first gill arch.

Scales: ctenoid; lateral line with 30 (f.1), 31 (f.8), 32 (f.23), 33 (f.11) or 34 (f.1);

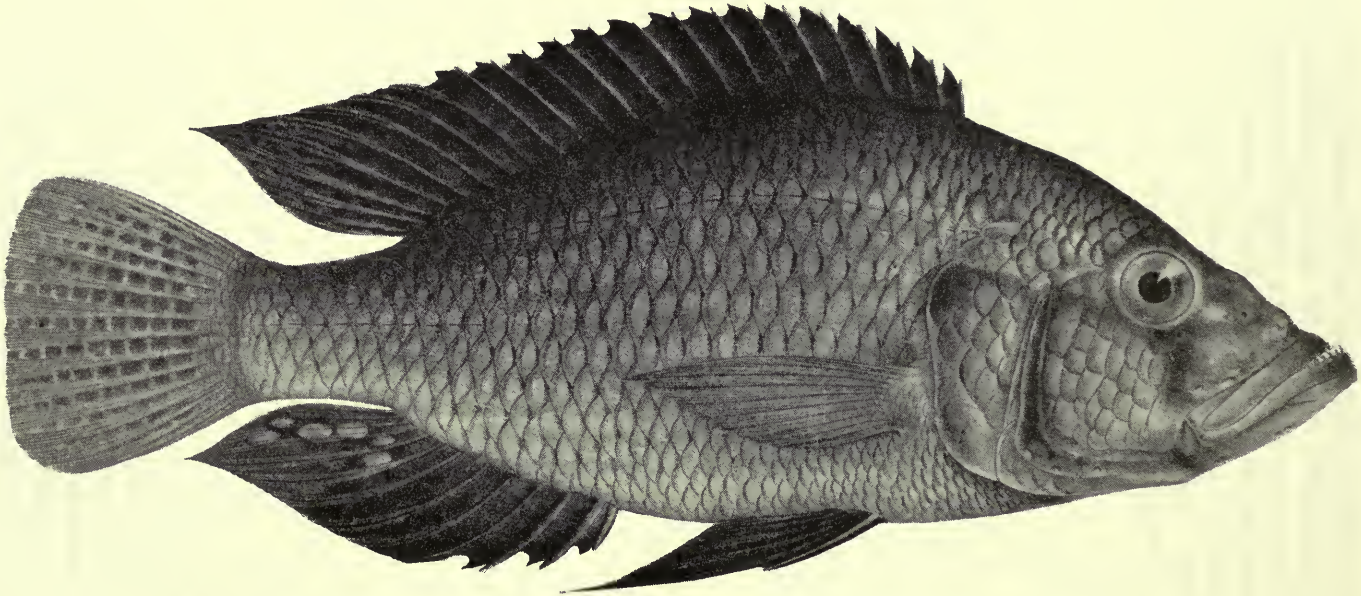

FIG. 1. *Haplochromis spekii*; lectotype; about ·77 times natural size. From Boulenger, *Fishes of the Nile.*

cheek with 3 (rare)-5 (mode 4) rows. Six to 8 (mode 7) between the upper lateral line and the dorsal fin origin, 5–9 (mode 8) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.12), 25 (f.30) or 26 (f.2) rays, comprising 14 (f.1), 15 (f.29) or 16 (f.14) spinous and 8 (f.1), 9 (f.21) or 10 (f.22) branched rays. Anal with 11 (f.2), 12 (f.30) or 13 (f.9) rays, comprising 3 spinous and 8 (f.2), 9 (f.30) or 10 (f.9) branched elements. Pectoral 27·0–33·3 (M = 29·3) per cent of standard length. Pelvics with the first and second branched rays produced, slightly so in females but the first ray protracted and thread-like in males. Caudal subtruncate, scaled on its basal half.

Teeth : In all specimens examined, both the inner and outer teeth are unicuspid, those of the outer row stout and strongly curved. The smallest fish (128 mm. S.L.) shows faint indications of lateral cusps on some teeth in the inner rows.

There are 44–70 (M = 55) teeth in the outer row of the upper jaw ; inner teeth in this jaw are arranged in 3–5 (usually 3 or 4) rows, and in the lower jaw in 2 or 3 (rarely 1 or 5) rows.

Osteology. The neurocranium of *H. spekii* is identical with that of *H. serranus*, that is, of the generalized predator type showing affinity with the skull of *H. guiarti* (see Greenwood, 1962).

The lower pharyngeal bone is triangular, its dentigerous surface broader than long. The lower pharyngeal teeth are relatively fine, cylindrical in cross-section and weakly bicuspid ; some teeth are almost uniscuspid, with the larger cusp elongate and conical. The teeth are arranged in 22–24 rows.

Vertebral counts (precaudal and caudal) for six specimens are 13 + 16 (f.3), 13 + 17 (f.2) and 12 + 17 (f.1).

Coloration. Live coloration is unknown. *Preserved specimens : Males* (*adult and sexually active*) *:* Ground colour overall dusky, including the entire head, both jaws and the branchiostegal membrane ; very faint indications of a broad midlateral stripe visible behind the operculum to the beginning of the caudal peduncle where it merges with the dark general body colour. Dorsal fin dark except for the distal third to half of the soft part which is hyaline with dark spots and dashes. Caudal dark on its basal two-thirds, yellowish distally. Anal light dusky except for the distal quarter to third of the soft part which is hyaline ; 4 or 5 moderately large ocelli (dead white), usually arranged in two rows or one irregular row. Pelvic fins dusky.

Adult (*but sexually quiescent males*) have a variable ground coloration which, however, is always lighter than that of sexually active fishes. The snout and jaws are darker than the flanks which vary from dusky to light golden-brown ; branchiostegal membrane dark, but sometimes only in the region below the operculum. Dorsal fin dark, the lappets black, and the soft part often with close-set dark spots or dashes. Anal variable, from dusky to yellowish ; ocelli whiteish-grey, 2–5 in number and arranged as in active fishes. Pelvics usually dusky but of a variable intensity ; when light, the pigment concentrated over the spine and the first two branched rays.

Females (*adult and juvenile*) *:* brownish above (and on the head and snout), shading to silvery-brown or greyish-silver on the lower flanks, belly, chest and operculum ; branchiostegal membrane greyish. A faint midlateral band (of variable depth and of irregular outline) runs from behind the operculum to the caudal fin origin ; there is also a very faint upper longitudinal band running slightly above the upper lateral line visible in some specimens. All fins are brownish-yellow the soft dorsal darkly maculate. Caudal dark brown on its proximal two-thirds (because of the dense maculation in that region).

Immature males are coloured like females except that the longitudinal stripes are more distinct, and some specimens have very faint traces of 4 or 5 vertical bars crossing the longitudinal stripes on the flanks ; these bars extend from the back to a level about half way towards the ventral outline. The pelvic fins are faintly sooty.

Ecology : Habitat. *Haplochromis spekii* occurs over both hard and soft substrates, but seems to show a slight preference for the former. Few specimens were collected from nets operated over exposed beaches, most coming from gill-nets set in sheltered areas where the water was 10–30 ft. deep. Some specimens were taken from more exposed areas, but not from deeper water.

Food. Of the 42 fishes examined (from 24 localities), 22 contained food. Twenty-one of these had fed exclusively on small fishes (identified in 8 guts as *Haplochromis* species, in a further 8 as Cichlidae, and in one as a cyprinid). The exceptional fish contained unidentifiable fish remains and fragments of an ephemeropteran larva (probably *Povilla adusta*).

Breeding. All specimens $<$ 150 mm. S.L. are immature, as is one specimen of 182 mm., but others $>$ 150 mm. are mature. Both sexes reach the same maximum adult size.

Affinities. The close relationship between *H. spekii* and *H. serranus* has been noted already (see above p. 33). There is complete overlap in most characters but the differential growth trends shown by two characters are such that this overlap is considerably reduced in fishes more than 120 mm. S.L. The two characters are depth of preorbital, and eye diameter as proportions of head length. In *H. spekii* both are, generally, larger than in *H. serranus* when specimens of the same size are compared. However, even in these characters there is still some overlap, and, from the sample studied, it seems likely that neither is a reliable diagnostic character when fishes $<$ 120 mm. S.L. are compared. The difference between *H. spekii* and *H. serranus* (in the size range 120–205 mm.) is perhaps best shown by the ratio of eye diameter to preorbital depth, *viz.*, 0·8–1·3 (mean 1·0) for *H. spekii*, and 1·1–1·5 (mean 1·3) for *H. serranus*.

Two other characters seem to show interspecific differences in their modal values. (i) In *H. serranus* the posterior tip of the maxilla usually lies below the eye or reaches to the vertical through the anterior orbital margin ; in *H. spekii* it rarely reaches as far posteriorly as the orbital margin (ii) *Haplochromis serranus* has a very prominent mental protuberance, but this bump is much weaker, if it is developed at all, in *H. spekii.* In many specimens of *H. serranus* the mental bump is so prominent that, in lateral view, the anterior margin of the dentary has a marked backward slope thus emphasizing the acuteness of the head profile ; in *H. spekii* the anterior margin of the dentary is, generally, almost perpendicular and so the tip of the head seems blunter than in *H. serranus.*

Unfortunately it is impossible to compare the live colours of adult males from the two species ; preserved coloration is similar. This information, together with more field data on niche preferences, and small specimens of *H. spekii*, will be necessary before the precise relationships (or perhaps conspecifity) of the two species can be determined. If *H. spekii* and *H. serranus* were allopatric it would be tempting, on the information available, to consider them conspecific. However, experience with other sympatric species in Lake Victoria suggests that such slight morphological differences as are known between *H. spekii* and *H. serranus* can be the only ones manifest by biologically distinct species.

Haplochromis spekii is more easily distinguished from other members of the *H. serranus* species complex.

From *H. victorianus* it is recognizable by its larger adult size (some *H. spekii* are juvenile at a size near the upper adult limits for *H. victorianus*), larger head (36·1–39·3, M = 37·4% S.L., *cf.* 33·5–36·0, M = 34·8%), deeper cheek (25·7–32·9, M = 29·5% head, *cf.* 22·5–26·2, M = 24·6%), longer lower jaw, (49·2–61·3, M = 53·8% head, *cf.* 44·0–51·8, M = 47·1%), smaller eye in fishes < 200 mm. S.L. (17·3–22·6, M = 20·0% head, *cf.* 21·7–26·2, M = 24·6%), shorter pectoral fin (21·4–28·9, M = 25·1% S.L., *cf.* 26·2–32·7, M = 30·4%), and by having fewer and more curved outer teeth in the upper jaw (44–70, M = 55 teeth, *cf.* 64–86, M = 74).

From *H. maculipinna*, *H. spekii* differs in its larger adult size, longer head (36·1–39·3, M = 37·4% S.L., *cf.* 32·6–37·0, M = 35·5%), longer snout (34·0–40·6, M = 36·8% head, *cf.* 30·3–37·0, M = 33·7%), deeper cheek (25·7–32·9, M = 29·5% head, *cf.* 23·2–29·8, M = 25·3%), longer lower jaw (49·2–61·3, M = 53·8% head, *cf.* 43·3–52·8, M = 48·3%), and lower eye/preorbital ratio (0·8–1·3, M = 1·0, *cf.* 1·3–1·6, M = 1·5).

Although *H. spekii* resembles *H. bartoni* a little more closely in morphometric characters than it does *H. victorianus*, the species show a greater difference in neurocranial form. The neurocrania of *H. victorianus* and *H. spekii* are virtually identical, but that of *H. bartoni* is nearest the typical " *prognathus* "-group type (see p. 109). Morphometrically, *H. spekii* differs from *H. bartoni* in having a broader interorbital region (22·0–26·0, M = 23·3% of head, *cf.* 17·0–21·0, M = 18·6%), and a somewhat smaller eye (17·3–22·6, M = 20·0% head, *cf.* 20·3–24·1, M = 22·5%). Also *H. spekii* has a lower modal number of spinous dorsal fin rays (15 *cf.* 16).

From the third member of the *H. serranus* species group, *H. nyanzae*, *H. spekii* differs in its larger adult size, larger head (36·1–39·3, M = 37·4% S.L., *cf.* 33·6–36·7, M = 35·4%), deeper cheek (25·7–32·9, M = 29·5% head, *cf.* 24·4–27·6, M = 25·9%), longer lower jaw (49·2–61·3, M = 53·8% head, *cf.* 45·0–51·6, M = 48·0%), and a lower modal number of spinous dorsal fin rays (15 *cf.* 16).

Although typical specimens of *H. spekii* and *H. gowersi* are not readily confused (compare text-fig. 1 with text fig. 13 in Greenwood, 1962) there is one specimen whose appearance is such that I am unable to place it in one species or the other ; it is even intermediate in the two quantifiable morphological characters (body depth and interorbital width) showing the greatest interspecific differences. *Haplochromis gowersi* and *H. spekii* differ markedly in neurocranial form, but without dissection this character cannot be checked with sufficient precision in the unique intermediate specimen. For the present, the possibility cannot be overruled that this fish is an interspecific hybrid.

Phyletically, *Haplochromis spekii* appears to be a derivative from an *H. serranus*-like ancestor, the principal difference between the species being the larger adult size attained by *H. spekii*.

Note : Gilchrist and Thompson (1917) record six specimens of *Pelmatochromis spekii* Blgr. from the Magalies river, Transvaal. I have not examined these specimens, but clearly they cannot be referred to *Haplochromis spekii* (Blgr.). Judging from their locality, it seems probable that they are specimens of *Chetia flaviventris* Trewavas. Dr. Trewavas is of a like opinion (personal communication).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.296 (Lectotype)	Bunjako	Degen
B.M. (N.H.) 1911.3.27.17 (Lectotype *H. serranoides*)	Victoria Nile	Melland
B.M. (N.H.) 1966.3.9.1–4, 20–21, 30–35, 39–49	Napoleon Gulf, near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.5	Beach near Nasu Point (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.11–14	Off S. tip of Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.28–29	Karenia, near Jinja (Napoleon Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.8–10	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.22	Thruston Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.27	Buka Bay (Buvuma Channel)	E.A.F.R.O.
	KENYA	
B.M. (N.H.) 1966.3.9.17–19	Kisumu (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.7	Naia Bay (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.15–16	Sagorony (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1928.5.24.413–5	Ulambwi Bay (Kavirondo Gulf)	Graham
	TANZANIA	
B.M. (N.H.) 1966.3.9.345	Beach near Majita	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.36–38	Between Ghogororo and Isanga River	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.6	Mwanza (Capri Bay)	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.23–26	Locality unknown	E.A.F.R.O.

Haplochromis pachycephalus sp. nov.

(Text-fig. 2)

Holotype : an adult male, 199 mm. standard length, from 40 ft. of water off Kazima island, Uganda. B.M. (N.H.) reg. no. 1966.2.21.9.

Description : based on the holotype and fourteen other specimens 150–232 mm. standard length.

Depth of body 36·5–42·5 (M = 39·1) per cent of standard length, length of head 35·6–39·5 (M = 36·3) per cent. Dorsal head profile straight to moderately concave, the concavity exaggerated by the prominent premaxillary pedicels ; nuchal region prominent and gently convex, prenuchal region sloping at 30°–35°. Cephalic lateral line pores large, especially on the preorbital and preopercular bones, less so on the dentary.

Preorbital depth 18·9–22·5 (M = 20·8) per cent of head, least interorbital width 24·6–31·3 (M = 27·8) per cent. Snout 1·1–1·4 (mode 1·2) times broader than long, its length 32·4–38·2 (M = 35·9) per cent of head ; eye diameter 18·8–22·2 (M = 20·6) per cent, depth of cheek 26·4–36·1 (M = 30·8) per cent.

Caudal peduncle 13·2–16·0 (M = 14·8) per cent of standard length, 1·0–1·3 (mode 1·2) times as long as deep.

Mouth oblique, sloping at an angle of 35°–45° (mode 40°). Jaws equal anteriorly or lower projecting slightly, its length 51·5–58·4 (M = 55·0) per cent of head, 1·5–1·9 (one specimen 2·2) times as long as broad. Posterior tip of maxilla reaching the vertical through the anterior orbital margin or nearly so.

Gill rakers : stout, the lower 1 or 2 sometimes reduced, the upper 3 or 4 sometimes expanded ; 8 or 9 (7 in one specimen) on the lower part of the first gill arch.

Scales ctenoid ; lateral line with 32 (f.3), 33 (f.4), 34 (f.4) or 35 (f.3), cheek with 5 or 6 (rarely 4) rows. Nine or 10 (less frequently 7, 8 or 10½) between the upper lateral line and the dorsal fin origin, 7 or 8 (less frequently 6 or 9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.6), 25 (f.6) or 26 (f.1) rays comprising 15 (f.9) or 16 (f.5) spinous and 8 (f.1), 9 (f.10) or 10 (f.3) branched rays. Anal with 11 (f.2) or 12 (f.12) rays, comprising 3 spines and 8 (f.2) or 9 (f.12) branched elements. Pectoral 21·6–30·9 (M = 24·6) per cent of standard length. Pelvics with the first branched ray produced in sexually active males, slightly so in females and quiescent males.

Teeth. The outer row in both jaws is composed of unicuspid, slender and slightly curved teeth. There are 60–80 (M = 70) teeth in the outer row of the upper jaw.

Teeth in the inner rows are small, unicuspid, curved (strongly so in the upper jaw) and implanted obliquely. There are 4 or 5 (less frequently 2 or 3) rows in the upper jaw and 2 or 3 (rarely 4) in the lower.

Osteology. No complete skeleton is available. The lower pharyngeal bone is triangular, with its dentigerous surface slightly broader than long (most markedly so in the smallest fish), or rarely, as long as broad. Lower pharyngeal teeth fairly coarse, their crowns weakly cuspidate and barely compressed ; some teeth in the two median rows are almost conical. The teeth are arranged in 18–22 rows.

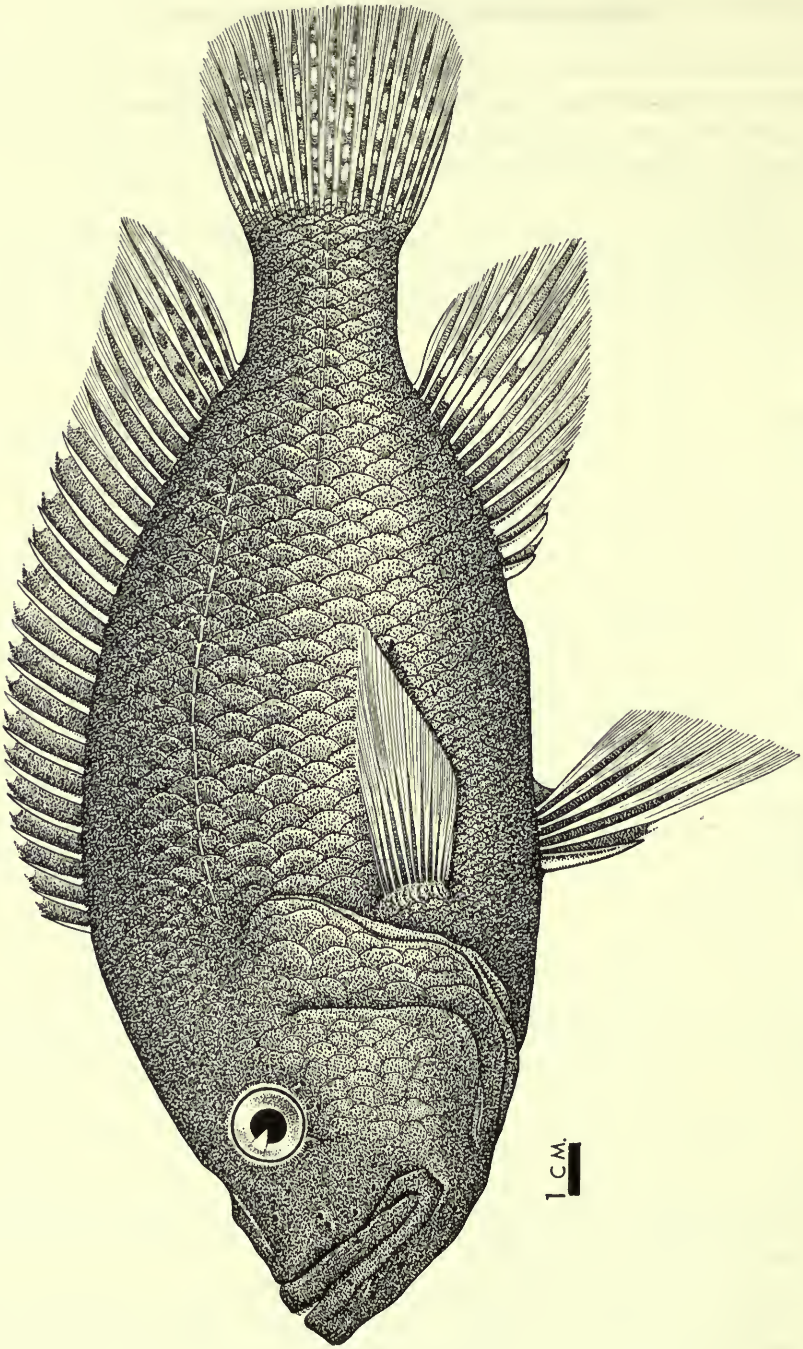

FIG. 2. *Haplochromis pachycephalus.* Drawn by Lavinia Beard.

Vertebral counts in 5 specimens are : 13 + 16 (f.3), 14 + 16 (f.1) and 14 + 17 (f.1).

Coloration : Live colours are unknown. *Preserved material : Adult males.* Ground colour variable and probably dependent on sexual state (also affected by preservation). Body greyish with black belly, chest and branchiostegal membrane, or the black replaced by a sooty-grey (in such specimens the branchiostegal membrane may be dark grey and flecked with sooty blotches) ; very faint traces of a broad midlateral stripe on the flank, originating behind the operculum and extending to the caudal fin origin. Dorsal fin greyish, dark lappets and maculae on the soft part. Caudal greyish, darkly maculate between the rays. Anal yellowish with a faintly sooty base, especially on the anterior part and around the ocelli ; the latter are dead-white, 5–9 (usually 5 or 6) in number and arranged in from 1 to 3 irregular rows. Pelvics blotched sooty to entirely black (the latter condition associated with the darkest body coloration).

Two fishes (both from the same net haul) are more sexually active than the others. Both are a very dark brown, almost uniformly so except for a black belly, chest and branchiostegal membrane. The spinous dorsal is a very dark brown (nearly black), the soft part is lighter and has a yellowish margin. Caudal light brown with lighter maculae on the basal three-quarters. Anal very faint pink, with a narrow black basal streak which expands in the region of the proximal row of ocelli and extends in amongst them ; the ocelli are whiteish.

Females (*adult but quiescent* ; based on two specimens only). Ground colour silver-grey becoming creamy on the chest and belly. Entire head (including the lower jaw) brownish with darker and irregular mottling. Body also mottled with sooty blotches, the effect being generally irregular except that on the flanks the blotches have some faint organisation into near vertical, broad bands extending from the dorsal outline to almost the ventral outline. There is some resemblance between this coloration and that of *H. cavifrons* (see Greenwood, 1962), although in *H. pachycephalus* the effect is less definitely that of freckling. Dorsal fin yellowish-grey with sooty freckling and blotching. Caudal densely and darkly blotched on its proximal third to half, greyish and darkly maculate distally. Anal greyish-yellow, with a narrow, sooty band along its base, and a duskiness over the spinous part ; both fishes have two large and distinct, dead white ocelli (an unusual feature in females). Pelvics hyaline with irregular sooty blotches.

Ecology. Habitat. The species is known from four localities ; all are some distance off-shore but close to islands. The specimens all came from nets set on a soft bottom at depths of 100–120 ft., except in one locality where the collection was made after the use of explosives. In this instance the charge was set off in about 40 ft. of water over a rock shelf with deeper water on its off-shore side.

Food. Of the 13 specimens examined (from 5 localities) six contained food in the stomach or intestines. All yielded macerated fish remains. Fragments of *Haplochromis* species were identified from three guts, a cyprinid fish in a fourth, and cichlid remains in two others.

Breeding. Little information is available about the breeding habits of *H. pachycephalus*. All specimens except the smallest (a male, 150 mm. S.L.) are mature. The two largest fishes (232 mm. and 228 mm. S.L.) are males.

Affinities. *Haplochromis pachycephalus* is, at least on superficial characters and those detectable on a radiograph, related to the *H. serranus* species group (see p. 109).

From *H. serranus*, *H. pachycephalus* is distinguished by its broader snout, broader interorbital (24·6–31·3, M = 27·8% head, *cf.* 20·4–26·8, M = 23·3%) and lower jaw (length/breadth ratio 1·5–1·9 *cf.* 1·8–2·5), and its smaller nuchal scales.

From *H. victorianus* it differs in its broader interorbital (24·6–31·3, M = 27·8% head, *cf.* 21·5–24·5, M = 22·6%), deeper cheek (26·4–36·1, M = 30·8% head *cf.* 22·5–26·2, M = 24·6%) and longer lower jaw (51·5–58·4, M = 55·0% head, *cf.* 44·0–51·8, M = 47·1%) ; the lower jaw is also broader in *H. pachycephalus.*

From *H. spekii* and *H. maculipinna*, the oblique mouth and broad snout of *H. pachycephalus* serve as immediately diagnostic characters, although the snout in *H. maculipinna* is broader than in other members of the " *serranus* "-group (being as much as 1·1 times broader than long, but generally as long as broad). As with other members of the group, *H. maculipinna* and *H. spekii* have a narrower interorbital region than *H. pachycephalus* ; *H. maculipinna* also has a larger eye (24·0–31·7, M = 26·3% head *cf.* 18·8–22·2, M = 20·6% in *H. pachycephalus*) but the larger adult size reached by *H. pachycephalus* may influence this character.

The same superficial characters (including the oblique mouth) serve to distinguish *H. pachycephalus* from *H. bartoni* and *H. nyanzae*, the former a member of the " *prognathus* " group, the latter a " *serranus* " group member.

Haplochromis boops and *H. thuragnathus* (both " *serranus* "-group species) closely resemble one another (see pp. 50) and *H. pachycephalus.* Both differ from *H. pachycephalus* in the following characters : a narrower interorbital, shorter snout, larger eye, and larger nuchal scales. All three species have the snout broader than it is long.

From the evidence available, *H. pachycephalus* would seem to be derived from an *H. serranus*-like ancestor, the principal morphological changes béing an increase in mouth size coupled with greater obliquity of the mouth angle. The larger cephalic lateral line pores of *H. pachycephalus* are probably correlated with the deep water habitat of the species (as compared with *H. serranus* and its immediate allies).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.175–177	Off S. tip of Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.174	Deep water off Dagusi Island	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.9 (Holotype)	Off Kazima Island	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.166–169, 171–173	Off Kazima Island	Uganda Fisheries Dept.
	TANZANIA	
B.M. (N.H.) 1966.3.9.170	Off Godziba Island	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.178	Locality unknown	E.A.F.R.O.

Haplochromis maculipinna (Pellegrin), 1913

(Text-fig. 3)

Paratilapia maculipinna Pellegrin, 1913 *Bull. Soc. Zool. France*, **37**, 311 ; *Idem*, 1914, in *Voyage de Ch. Alluaud et R. Jeannel en Afrique Occidental*, 16, Pl. 1, fig. 1, Paris.
Paratilapia prognatha (part) : Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 333.
Haplochromis maculipinna : Regan, 1922, *Proc. zool. Soc. Londn.*, 177, fig. 5.

HOLOTYPE : a fish 122·0 mm. S.L. (Paris Museum No. 12–258) from Port Florence (Kavirondo Gulf) collected by Alluaud and Jeannel.

This specimen differs from all others now included in the species by its much larger eye. In other characters, however, it agrees with these specimens and differs from the few other Victoria *Haplochromis* species characterized by large eyes.

DESCRIPTION : based on 33 specimens (including the holotype), 91·5–166 mm. S.L.

Depth of body 33·3–37·0 (M = 35·9) per cent of standard length, length of head 32·6–37·0 (M = 35·5) per cent. Dorsal head profile straight or slightly concave in those fishes with prominent premaxillary pedicels, sloping at 30°–35°.

Preorbital depth 16·4–20·4 (M = 18·2) per cent of head, least interorbital width 20·7–25·5 (M = 22·8) per cent. Snout as long as broad to 1·1 times broader than long, its length 30·3–37·0 (M = 33·7) per cent of head, eye diameter 24·0–29·2 (31·7 in the type), mean 26·3 per cent, ratio of eye/preorbital 1·3–1·6 (M = 1·5) but 1·9 in the type ; depth of cheek 23·2–29·8 (M = 25·3) per cent.

Caudal peduncle 14·5–18·8 (M = 16·3) per cent of standard length, 1·2–1·8 (modal range 1·2–1·5) times as long as deep.

Mouth moderately oblique, sloping upwards at 35°–40°, lower jaw projecting slightly to strongly, its length 43·3–52·8 (M = 48·0) per cent of head, 1·6–2·3 (modal

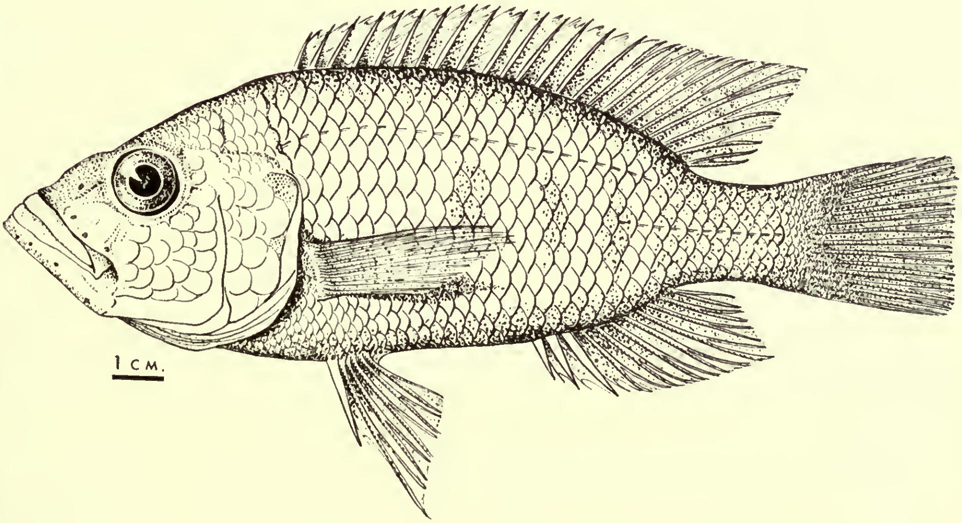

FIG. 3. *Haplochromis maculipinna.* Drawn by Barbara Williams.

range 1·7–2·1) times as long as broad. Lips not noticeably thickened, premaxilla not expanded medially. Posteriorly tip of the maxilla not quite reaching the vertical through the anterior orbital margin.

Gill rakers : moderately stout, the lower 1–3 reduced, the upper 2–5 flat and sometimes divided ; 8–11 (mode 10) on the lower part of the first arch.

Scales : ctenoid ; lateral line with 31 (f.1), 32 (f.15), 33 (f.15) or 34 (f.2), cheek with 3–5 (mode 3) rows. Five and a half (rare) to 8 (modal range 6–7) scales between the upper lateral line and the dorsal fin origin, 5½ (rare)–9 (modal range 7–8) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.5), 25 (f.26) or 26 (f.2) rays, comprising 14 (f.1), 15 (f.24) or 16 (f.8) spinous and 9 (f.11) or 10 (f.22) branched rays. Anal with 11 (f.3), 12 (f.27) or 13 (f.3) rays, comprising 3 spines and 11 (f.3), 12 (f.27) or 13 (f.3) branched elements. Pectoral 23·0–31·0 (M = 26·4) per cent of standard length. Pelvics with the first two branched rays produced in both sexes, but markedly elongate in adult males. Caudal truncate to subtruncate.

Teeth. Except in the smallest specimen (91·5 mm. S.L.), the outer teeth are unicuspid ; in the exceptional fish most teeth are weakly bicuspid but a few are unicuspids. All outer teeth are slightly curved and slender, the curvature being most marked in teeth situated laterally and posterolaterally ; teeth situated posterolaterally in the upper jaw are the smallest and finest. There are 50–80 (M = 62) teeth in the outer row of the upper jaw.

Teeth in the inner rows are more variable in form, and there is no clear-cut correlation between tooth form and the fish's size. The smallest specimen has only tricuspid inner teeth ; other and larger fishes may have only weakly tricuspids in both jaws, or tricuspid teeth predominating in both jaws but some unicuspids occurring in the lower jaw, or an admixture of tri- and unicuspids (the latter predominating) in the upper jaw and only unicuspids in the lower, or a mixture of tri- and unicuspids in both jaws, or unicuspids in the upper jaw and an admixture in the lower, or only unicuspids in both jaws. Some of the largest fishes fall in either the mixed uni- and tricuspid category or in the purely unicuspid one.

The inner teeth are arranged in 1 (rare)—4 (modes 2 and 3) rows in the upper jaw, and 2 (less commonly 1 or 3) rows in the lower.

Osteology. The neurocranium of *H. maculipinna* is virtually identical with that of *H. serranus*, differing only in having a relatively lower supraoccipital crest. The premaxilla, dentary and suspensorium are also like those of *H. serranus*, except that the dentary is somewhat deeper and shorter in *H. maculipinna.*

The lower pharyngeal bone is triangular and rather fine ; the dentigerous surface is slightly broader than long. Lower pharyngeal teeth are slender and distinctly cuspidate, those of the two median rows are the coarsest ; the teeth are arranged in 20–24 rows.

Vertebral counts for seven specimens are : 13 + 16 (f.1) ; 13 + 17 (f.3) ; 14 + 16 (f.2) and 14 + 17 (f.1), giving totals of 29 to 31.

Coloration : Live colours are unknown. *Preserved specimens : Males (adult and sexually active) :* ground colour very dark brown, almost black, with a golden underlay on the flanks and operculum, and a sooty overlay on the chest. Head, including the lower jaw, dark but lips light brown. A very faint, but broad, lachrymal stripe runs from the antroventral margin of the orbit to the angle of the lower jaw. The branchiostegal membrane is black. Dorsal fin almost uniformly dark sooty, the lappets black. Caudal dark on its proximal three-quarters, dusky distally. Anal dusky, but with a black band along its base, the band expanding anteriorly to cover most of the spinous part of the fin, which is black; two or three large greyish ocelli are present. Pelvics black to dusky.

Males (*adult but sexually quiescent*): ground colour dark golden brown, lightest on the anterior flanks. Head dark brown, with a distinct, narrow lachrymal stripe from orbit to angle of lower jaw, and a narrow black vertical bar on the ascending preopercular limb; branchiostegal membrane greyish-brown. Dorsal fin yellowish-grey, with black lappets, and the membrane between the branched rays dark grey-brown; the pigment often broken into discrete maculae between the last three or four branched rays. Caudal dark yellowish-grey. Anal uniformly yellowish, with two or three faint, whiteish ocelli. Pelvics dark on the anterior third, otherwise yellowish to hyaline.

Males (*immature*): ground colour light brown on the flanks and belly, darker above the upper lateral line and on the dorsum of the head; the branchiostegal membrane is light brown-grey, and a faint lachrymal stripe is visible. On the flanks there is a trace of an interrupted, dark midlateral band on the anterior half of the body, and a continuous band on the posterior half, extending to the caudal origin. Dorsal fin yellowish-brown, the lappets dark, as are the maculae between the branched rays. Caudal yellowish-brown, with dark elongate blotches between the rays. Anal uniformly yellowish-brown, with two or three, distinct and dusky-grey ocelli. Pelvics yellowish with a faint dusky overlay, especially over the anterior part of the fin.

Females (*adult and juvenile*): ground colour golden brown, darker on the upper half of the body, and the dorsal surface of the head; faint traces of a rather broad lachrymal stripe are often visible, the stripe generally not extending to below the level of the maxilla, but reaching the angle of the lower jaw in some specimens. Faint traces of an interrupted midlateral band on the anterior half of the body, and a continuous band on the posterior half are often visible; in some specimens no lateral band is visible, and in others the band is continuous except for a short break at about its midpoint. A few specimens show indications of a much interrupted band (really a series of 6 or 7 broad blotches) running slightly above the upper lateral line on the anterior half of the flanks, and on the lateral line posteriorly. Dorsal fin yellowish, usually darker between the posterior spines, and darkly maculate on the soft part, but uniformly yellowish with very faint maculations posteriorly in others. Anal, caudal and pelvic fins uniformly yellowish.

Ecology. Although some individuals occur over sandy, exposed and wave-washed beaches, members of this species are commoner in sheltered gulfs and bays where the water is from 10–30 ft. deep and the substrate is either soft mud or sand and shingle; a few specimens are from deeper water (35–40 ft.) near off-shore islands.

Food. Eleven of the 30 specimens examined (from 16 localities) contained food in the stomach and intestines. Seven fishes yielded fragmentary fish remains (identified as a cyprinid in one, and as *Haplochromis* species in two others), three contained fragmentary insect remains (probably larval Ephemeroptera), and one bottom debris.

Breeding. Little information is available ; most specimens less than 140 mm. S.L. are immature, as is one slightly larger individual (145 mm.). Both sexes attain the same maximum adult size.

Affinities. In both its gross and detailed morphology *H. maculipinna* shows affinity with the " *serranus* " species group, i.e. *H. serranus*, *H. victorianus*, *H. spekii*, and their deep water relatives *H. pachycephalus*, *H. boops* and *H. thuragnathus*. Criteria for distinguishing *H. maculipinna* from all but the first two species are considered under the descriptions of those species (see pp. 37, 42, 49 and 51 for the species respectively).

From *H. serranus*, *H. maculipinna* is distinguished by its larger eye (24·0–31·7, M = 26·3% head, *cf.* 20·4–26·0, M = 23·3%), shorter and more oblique lower jaw (43·3–52·8, M = 48·3% head, *cf.* 47·7–60·0, M = 54·3%), and higher eye/preorbital ratio (1·3–1·6, M = 1·5 *cf.* 1·1–1·5, M = 1·3).

From *H. victorianus*, it differs in its larger eye (24·0–31·7, M = 26·3% head *cf.* 21·7–25·5 M = 23·6%), higher eye/preorbital ratio (1·3–1·6, M = 1·5, *cf.* 1·1–1·3, M = 1·2), more oblique lower jaw (sloping at 30°–35° *cf.* horizontal or very slightly oblique) and its fewer and finer outer teeth (50–80, M = 62, *cf.* 64–86, M = 74 teeth in the upper jaw).

The close resemblance between *H. maculipinna* and these two species is obvious, and is greater than the resemblance between *H. maculipinna* and other members of the " *serranus* " group.

There are two other species, *H. nyanzae* and *H. bartoni* which, at least superficially, resemble members of the " *serranus* " group although *H. bartoni* seems to belong to a different phyletic line (see p. 109).

Haplochromis maculipinna differs from *H. nyanzae* in its larger eye (24·0–31·7, M = 26·3% head, *cf.* 19·1–24·0, M = 22·1%) and higher eye/preorbital ratio (1·3–1·6, M = 1·5, *cf.* 1·1–1·3, M = 1·2), and by its finer and less curved outer teeth.

From *H. bartoni*, it differs in having a shorter head (32·6–37·0, M = 35·5% standard length, *cf.* 36·2–39·7, M = 37·5%), broader interorbital (20·7–25·5, M = 22·8% head, *cf.* 17·0–21·0, M = 18·6%) and shorter, more oblique lower jaw (43·3–52·8, M = 48·3% head, *cf.* 50·8–57·0, M = 52·5%). Neurocranial form differs in the two species, that of *H. maculipinna* being of the " *serranus* " type, and that of *H. bartoni* being of the " *prognathus* " type (see p. 110).

Resemblances between *H. maculipinna* and *H. acidens* are discussed on p. 76. It seems unlikely that the species are closely related.

Phyletically, *H. maculipinna* was probably derived from a *H. serranus*-like ancestor.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.263	Bunjako	Degen
B.M. (N.H.) 1966.3.9.145–151	Napoleon Gulf, near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.132–134	Beach near Nasu Point (Buvuma channel) . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.135–144	Near Ramafuta Island (Buvuma Channel) . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.129–131	Between Yempita and Busiri Island (Buvuma Channel) .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9. 124–6	Buka Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.123	Fielding Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.128	Kazima Island (near Entebbe) .	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.127	Pilkington Bay	E.A.F.R.O.
	KENYA	
Paris Museum 12–258 (Holotype)	Port Florence (Kavirondo Gulf) .	Alluaud & Jeannel
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.122	Locality unknown . . .	E.A.F.R.O.

Haplochromis boops sp. nov.

(Text-fig. 4)

HOLOTYPE : an adult male, 190 mm. standard length, from 120 ft. of water, off the southern tip of Buvuma island (Uganda). B.M. (N.H.) reg. no. 1966.2.21.7.

DESCRIPTION : based on three specimens, 179–194 mm. standard length ; all are males.

Depth of body 40·5–42·3 per cent of standard length, length of head 35·3–36·1 per cent. Dorsal head profile straight, sloping steeply at 40°–50° ; premaxillary pedicels not prominent. Cephalic lateral line pores enlarged, especially those on the preoperculum, preorbital and dentary.

Preorbital depth 17·8–18·6 per cent of head, least interorbital width 21·7–25·7 per cent. Snout 1·2–1·3 times as broad as long, its length 32·6–32·8 per cent of head ; diameter of eye 23·9–25·7, depth of cheek 28·0–30·0 per cent.

Caudal peduncle 14·8–15·6 per cent of standard length, 1·2 times as long as deep.

Mouth somewhat oblique, sloping at 30°–35° (a horizontal line drawn through the tip of the lower jaw passes below the orbit). Jaws equal anteriorly or the lower projecting slightly, its length 50·0–52·5 per cent of head, 1·5–1·8 times as long as broad. Posterior tip of the maxilla reaching to a point below the anterior part of the eye.

Gill rakers : variable in form, from slender to stout, even in one individual ; the upper 3 rakers branched in one fish. Eight or 9 on the lower part of the first gill arch.

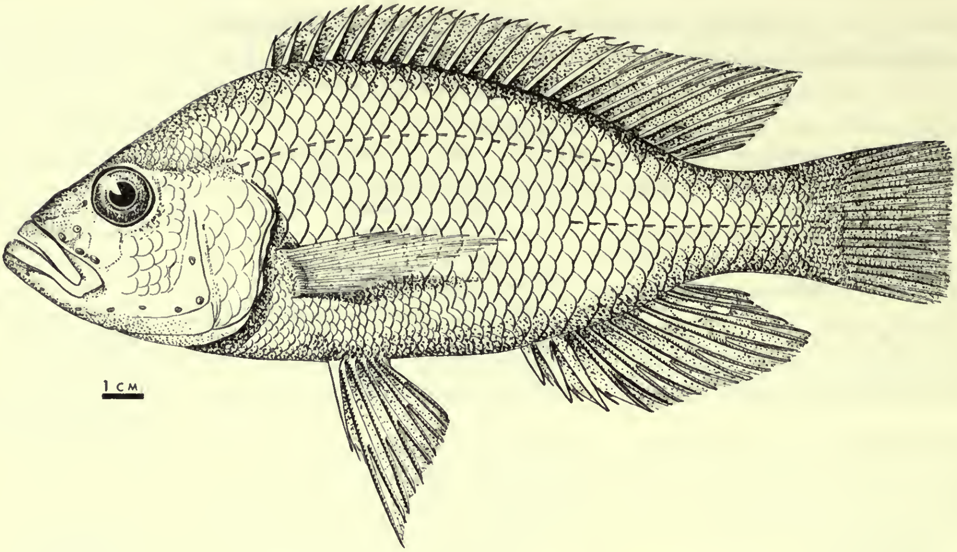

FIG. 4. *Haplochromis boops.* Drawn by Barbara Williams

Scales : ctenoid ; lateral line with 33 (f.2) or 34 scales, cheek with 4 (f.2) or 5 rows. Seven or 8 scales between the dorsal fin origin and the upper lateral line, 7 or 8 between the pectoral and pelvic fin bases.

Fins : Dorsal with 15 spines and 9 (f.1) or 10 (f.2) branched rays, anal with 3 spines and 8 (f.1) or 9 (f.2) branched rays. Pectoral 25·2–32·6 per cent of standard length. Pelvics with the first branched ray produced. Caudal subtruncate.

Teeth : In the outer row of both jaws, the teeth are small, curved and slender, with about 70 in the upper jaw.

Inner teeth, arranged in three rows in both jaws, are unicuspid, small and slightly curved.

Osteology. No complete skeleton is available, but radiographs have been studied. The lower pharyngeal bone is triangular, with its dentigerous surface broader than long. Lower pharyngeal teeth are relatively stout with cylindrical necks, and compressed, weakly cuspidate crowns. The teeth are arranged in 20–22 irregular rows. The vertebral counts in three specimens are : 13 + 16 (f.1) and 13 + 17 (f.2).

Coloration : Live colours are unknown. *Preserved material : Males (adult and sexually active) :* ground colour almost uniformly black (including the head, snout, branchiostegal membrane and belly) but with a brownish tinge. Dorsal with the spinous part blotched black on dark grey (black predominating), soft part black but with a hyaline band originating at the level of the tip of the last spine thence passing slightly downwards to end at a point about one third of the distance from the tip of the last branched ray ; the dark band distal to the hyaline strip is less intense than that along the basal part of the fin. Anal black over the spines and along the basal third of the whole fin, remainder sooty ; the five grey-white ocelli are arranged in two rows. Pelvic fins black.

No female specimens are available.

Ecology. Habitat. The two localities from which *H. boops* is known are in deep water (about 120 ft.) near islands and over mud substrates.

Food. Two specimens provided data on feeding habits. In both, the stomach had been everted, but fragments of macerated fish were collected from the pharynx and amongst the folds of the stomach wall. Judging from the scales and fin spines collected in this way, the fishes had fed on *Haplochromis*.

Breeding. All three specimens are adult, sexually active males.

Affinities. Haplochromis boops most closely resembles *H. thuragnathus*; at present the species can only be distinguished by the more oblique jaw of the latter (see p. 51).

Like *H. thuragnathus*, *H. boops* appears to be a derivative of the *H. serranus* species group, probably from an ancestor resembling *H. maculipinna*. From that species *H. boops* is immediately distinguished by its broader snout (broader than long, *cf.* as long as broad), enlarged cephalic lateral line pores, and deeper body.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.182	Near Dagusi Island . . .	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.7 (Holotype)	Off southern tip of Buvuma Island	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.181	Off southern tip of Buvuma Island	E.A.F.R.O.

Haplochromis thuragnathus sp. nov.

HOLOTYPE: an adult male, 191 mm. standard length, from 120 ft. of water off the southern end of Buvuma island (Uganda); B.M. (N.H.) reg. no. 1966.2.21.8.

DESCRIPTION: based on three specimens, 191 and 200 mm. standard length. Since so few specimens are available, only ranges for morphometric characters are given.

Depth of body 39·8–41·5 per cent of standard length, length of head 34·5–35·1 per cent. Dorsal head profile slightly concave, sloping at about 30°. Cephalic lateral line pores are enlarged, especially those on the preorbital and preopercular bones.

Preorbital depth 16·4–18·8 per cent of head, least interorbital width 23·2–24·5 per cent. Snout 1·2–1·3 times as broad as long, its length 30·9–31·8 per cent of head, eye diameter 24·6–26·8, depth of cheek 27·4–29·8 per cent.

Caudal peduncle 16·0–17.7 per cent of standard length, 1·3–1·4 times as long as deep.

Mouth oblique, sloping at 40°–45°, the jaws equal anteriorly or the lower projecting slightly, length of lower jaw 53·6–56·5 per cent of head, 1·7–2·2 times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or to below the anterior part of the eye. A horizontal drawn anteroposteriorly through the tip of the lower jaw passes through the lower part of the eye (*cf. H. boops* where the line passes below the orbit.)

Gill rakers : stout, 9 on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 32, 33 or 34 scales, cheek with 2–4 rows. Seven or 7½ scales between the upper lateral line and the dorsal fin origin, 7 between the pectoral and pelvic fin bases.

Fins. Dorsal with 16 spines and 9 branched rays. Anal with 3 spines and 8 branched rays. Pectoral 26·0–30·0 per cent of standard length. Pelvics with the first branched ray produced, proportionately more so in males. Caudal subtruncate.

Teeth. In the outer row of both jaws, the teeth are unicuspid, small and curved ; there are 70 teeth in the upper jaw.

Inner teeth are unicuspid, small and slightly curved, and are arranged in 3 series in the upper jaw, and 2 or 3 series in the lower.

Osteology. No complete skeleton is available, but radiographs of the three specimens were examined. The lower pharyngeal bone is triangular, its dentigerous surface broader than long. The pharyngeal teeth are relatively coarse, with cylindrical necks and compressed, weakly biscuspid crowns, and are arranged in 20–22 irregular rows. Vertebral counts for all three specimens are : 13 + 17.

Coloration : Live colours are unknown. *Preserved material : Males* (*adult and sexually active*) *:* ground colour sooty over dark brown dorsally (including the head), silvery on the belly and midflank ; chest and belly darker (*i.e.* sootier), almost black There is a faint golden flush on the operculum, but it is confined to the centre of this bone and is outlined with a broad dark margin. On the flank of the lighter coloured fish are traces of a broad, dark midlateral stripe. The branchiostegal membrane is black except for its posterior and ventral margins which are greyish. Dorsal fin black except for the distal half of the soft part which is greyish. Caudal dark, but lighter towards the distal margin. Anal black on its basal half and over the spinous portion ; one large white ocellus is present in the fish with the smaller testes, but the other has 8 ocelli arranged in two irregular rows. Pelvic fins black.

Female (*quiescent*) *:* ground colour brownish, darker on back, head and snout, lighter (with silvery background) on flanks and belly ; very faint traces of a broad (three scale rows deep) interrupted midlateral band on the flanks. Operculum silvery ; a faint, dark lachrymal stripe from the orbit to behind the posterior tip of the maxilla. All fins grey-brown, the anal with 3 small, whiteish spots in the position occupied by the ocelli in males ; pelvics more grey than brown.

Ecology. Habitat. All three specimens came from nets set on the mud-bottom in water about 120 ft. deep off the southern tip of Buvuma island.

Food. Two of the three specimens examined had fragments of small *Haplochromis* species in the stomach and intestines ; the guts of the third fish were empty.

Breeding. The three specimens are adults, the two males sexually active, the female quiescent.

Affinities. Haplochromis thuragnathus is most closely related to *H. boops.* Indeed, when more material is available it may be shown that the species are not distinct. Information on the live coloration of adult males of the two species would be extremely useful in establishing their status. From *H. boops, H. thuragnathus* is distinguished by its more oblique lower jaw. If a horizontal line is drawn posteriorly from the tip of the lower jaw (when closed) it passes through the lower part of the eye in *H. thuragnathus*, but below the eye in *H. boops*.

A third member of this group, *H. pachycephalus*, is compared with *H. thuragnathus*. on p. 42.

It seems probable that *H. thuragnathus* was derived from an *H. maculipinna*-like ancestor, and more particularly from one like *H. boops* (assuming that the more oblique lower jaw is a derived condition). Like *H. pachycephalus* and *H. boops*, *Haplochromis thuragnathus* differs from other members of the "*serranus*" phyletic assemblage by its broad snout, and from individual members of the group by various combinations of morphometric characters (see descriptions of *H. serranus* and *H. victorianus* in Greenwood, 1962, and of *H. maculipinna* and *H. spekii* on pp. 46 and 37 above).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.2.21.8	Off S. tip of Ramafuta Island .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.179–180	Off S. tip of Ramafuta Island .	E.A.F.R.O.

Haplochromis xenostoma Regan, 1922

(Text-figs. 5 and 6)

Paratilapia prognatha (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 333 (two specimens, one collected by Sir H. H. Johnston, the other from Entebbe and collected by Degen).
Haplochromis xenostoma, Regan, 1922, *Proc. zool. Soc. Londn.*, 185, fig. 10.

LECTOTYPE: an immature fish 104·0 mm. S.L. (B.M. [N.H.]reg. no. 1901.6.24.90) collected by Sir H. H. Johnston from Lake Victoria (locality unspecified).

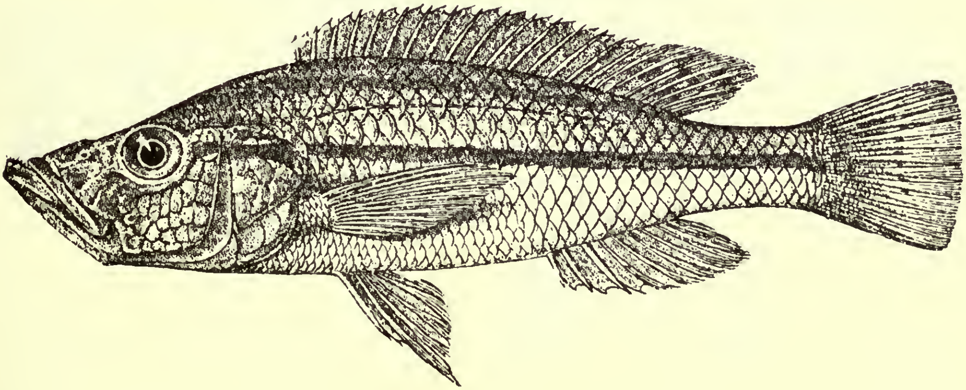

FIG. 5. *Haplochromis xenostoma*, juvenile; lectotype, about natural size. From Regan, *Proc. zool. Soc.*

Description: based on 27 specimens (including the lectotype) 99–203 mm. S.L. but excluding the paralectotype. Only four specimens are less than 140 mm. S.L. (99, 104 [lectotype], 106 and 119 mm. respectively); on the basis of this material it appears that body depth and lower jaw length may show some slight positive allometry.

Depth of body 27·0–40·0 (M = 36·5) per cent of standard length, head length 34·6–39·7 (M = 37·3) per cent. Dorsal head profile straight or slightly convex, sloping at an angle of 20°–30°, its outline noticeably interrupted by the prominent premaxillary pedicels which give it a stepped appearance.

Preorbital depth 17·5–22·7 (M = 20·3) per cent of head, least interorbital width 20·4–27·5 (M = 24·5) per cent. Snout 1·2–1·5 times as long as broad, its length 34·2–39·2 (M = 37·4) per cent of head; eye diameter 18·5–24·3 (M = 19·7), depth of cheek 24·3–30·8 (M = 28·1) per cent.

Caudal peduncle 14·3–18·3 (M = 15·3) per cent of standard length, 1·1–1·7 (modal range 1·3–1·4) times as long as deep; the lectotype has an unusually shallow peduncle (ratio 1·7).

Mouth very oblique, sloping at an angle of 40°–45°, the lower jaw strongly projecting beyond the upper, its length 50·0–62·0 (M = 57·0) per cent of head and 2·0 (rarely)–3·0 times as long as broad (modal range 2·3–2·5). Posterior tip of maxilla generally not reaching the vertical through the anterior orbital margin, but reaching this point in a few specimens.

Gill rakers: short and stout, or relatively slender and elongate, the lower one or two reduced; 8–10 (mode 9) on the lower part of the first gill arch.

Scales: ctenoid; lateral line with 29 (f.1), 31 (f.10), 32 (f.12), 33 (f.3) or 34 (f.1), cheek with 3 (mode) or 4 rows. Six or 7 (rarely 5 or 8) scales between the upper

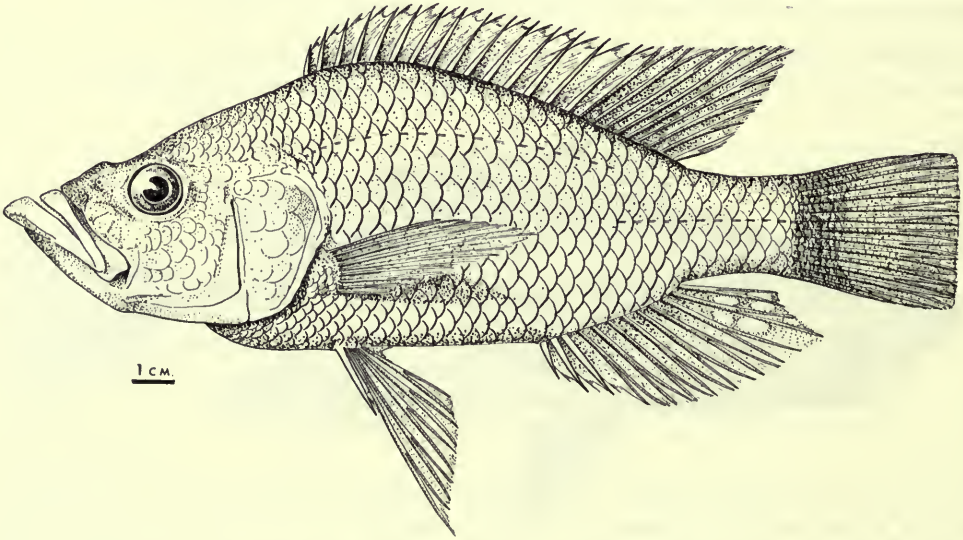

Fig. 6. *Haplochromis xenostoma* adult. Drawn by Barbara Williams.

lateral line and the dorsal fin origin, 5–7 (rarely 8) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.9), 25 (f.17) or 26 (f.1) rays, comprising 14 (f.1), 15 (f.22) or 16 (f.4) spinous and 9 (f.11) or 10 (f.16) branched rays. Anal with 11 (f.11) or 12 (f.16) rays, comprising 3 spines and 8 or 9 branched elements. Pelvics with the first two branched rays produced in both sexes but proportionately more so in adult males. Pectoral 24·2–33·0 (M = 28·0) per cent of standard length. Caudal truncate, scaled on its proximal half or slightly more.

Teeth. In fishes 119 mm. S.L. and above, the outer teeth in both jaws are unicuspid and moderately stout (but occasionally slender), those in the anterior part of the jaw with a slight inward curvature, and those situated laterally and posteriorly even less curved. The lectotype (104 mm. S.L.) has an outer dentition like that of larger fishes, but in the other small fishes (88–106 mm. S.L.) the outer teeth are distinctly bicuspid anteriorly, and weakly bicuspid laterally and posterolaterally. There are 56–94 (M = 82) teeth in the outer row of the upper jaw.

Fishes less than 106 mm. S.L. have either only tricuspid teeth or a mixture of uni- and tricuspids (some weakly so) in the inner series. A specimen 119 mm. S.L. has predominantly bicuspid teeth in the upper jaw, but in the lower jaw the first row of inner teeth is composed of unicuspids, and the other rows of tri- and weakly tricuspids. In all other specimens the inner rows are composed entirely of unicuspids. Inner teeth may be implanted somewhat obliquely so as to be medially inclined. The teeth in the outermost row of the upper inner series are often noticeably larger than their congeners. There are 2–5 rows of inner teeth in the upper jaw, and 2 or 3 (rarely 4) in the lower.

Osteology. The neurocranium of *H. xenostoma* is similar to that of *H. victorianus* (see Greenwood, 1962) but has a longer preorbital face (30·3 per cent of neurocranial length *cf.* 26·0 per cent ; the preorbital face being measured from the anterior tip of the vomer to the lateral ethmoid) ; the neurocrania of the two species also differ in that the supraoccipital crest of *H. xenostoma* is relatively higher and more pointed than in *H. victorianus.* It differs from the neurocranium of *H. serranus* (as it does from that of *H. victorianus*) in its less curved dorsal profile, and its longer preorbital face.

The very oblique and prognathous lower jaw is reflected in certain details of the suspensorium (text-fig. 7) ; all comparisons were made with *H. serranus*, a species

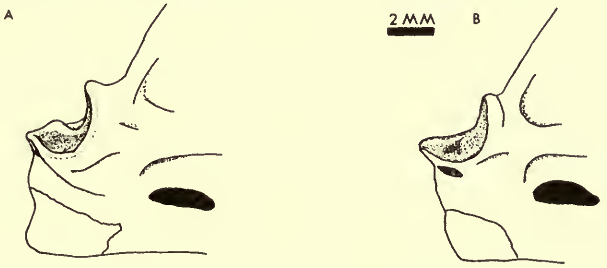

FIG. 7. Articulatory facet for the quadrate on the articular of (A) *H. xenostoma*, and (B) *H. serranus*.

with a moderately oblique jaw angle of 20°–30°. In *H. xenostoma* the articulatory surface of the articular is deeper and more nearly " U " shaped in lateral view; it lacks the posterior prolongation of its ventral border, but has a marked, near-conical eminence developed postero-medially. All these differences seem to be associated with the oblique angle of the jaw at rest, and the wide angle through which it can be abducted when the mouth is maximally protruded. The small eminence appears to function as a control for the degree of lateral movement of the dentary, particularly when that bone is dropped almost to the horizontal. The posterior vertical limb of the articular in *H. xenostoma* slopes forward at a much greater angle from the perpendicular, thus providing more space between this bone and the suspensorium.

On the basis of my material (two skeletons of *H. xenostoma*, and one each of *H. serranus* and *H. victorianus*) it appears that the horizontal length of the suspensorium (as measured in a horizontal plane from the mid-point of the hyomandibular to the articular surface of the quadrate) is greater in *H. xenostoma* than in the other two species. This could account, at least partly, for the greater prognacity of this species, whose lower jaw has the same relative length as that of *H. serranus* and *H. victorianus*. The angle of the hyomandibular relative to the perpendicular is similar in all three species.

The premaxilla has a slight median expansion of its dentigerous surface, and the pedicels are relatively shorter than those of *H. serranus*.

As compared with the dentary of *H. serranus* and *H. victorianus*, that of *H. xenostoma* is deeper and stouter, and the dentigerous surface has a more pronounced upward sweep towards the coronoid region.

The lower pharyngeal bone is triangular, and fairly stout; the dentigerous area is as long as broad or very slightly broader than long. Lower pharyngeal teeth are variable in form, usually with coarse, cylindrical necks and compressed, weakly cuspidate crowns; in some fishes, however, the crowns are distinctly cuspidate. Less commonly, the teeth are slender and compressed, with very weakly cuspidate crowns. The teeth are arranged in 22–24 rows.

Vertebral counts in 7 specimens are: 13 + 15 (f.1), 13 + 16 (f.5) and 13 + 17 (f.1), giving totals of 28–30.

Coloration: Live colours are known only for a single *juvenile female*; ground coloration silvery, shading to yellowish-grey dorsally, the dorsal surface of the snout dark grey. Dorsal fin dark hyaline, pelvics hyaline, anal yellow, caudal yellowish-grey. *Preserved coloration: Males* (*adult and sexually active*) have the ground coloration generally dusky over dark brown dorsally, and silver on the flanks and belly, the latter region together with the chest often with a dusky overlay; lower jaw and entire branchiostegal membrane also sooty. Snout and preoperculum sooty, but the upper lip is dark brown; operculum with a faint golden flush. A faint but dark and broad midlateral stripe runs along the flank from the posterior margin of the preoperculum to the caudal fin origin. Dorsal fin yellow-brown, with a sooty overlay on the spinous part, and black lappets; soft part with dark spots and dashes. Caudal dusky on its proximal threequarters, yellowish-brown distally. Anal light brownish-yellow, with a thin dark line along the base, and black lappets;

3 or 4 large, darkor whitesh ocelli are present, each with a narrow black outline. The ocelli are arranged in one or two rows. Pelvics entirely dusky.

Males (*adult but quiescent*) *:* have essentially the same coloration as active males, but some are lighter (that is, with more silvery flanks, and greyish branchiostegal membrane).

Females (*adult, and at various degrees of sexual activity*). Greyish-brown above, shading through silvery-grey on the flanks to gold below ; snout and preorbital region dark. On the flanks, a faint dark midlateral band (as in males) may be visible, and in addition, a fainter upper band running just above the upper lateral line. Dorsal fin yellowish-grey with a sooty overlay on the spinous part, and with black lappets ; soft dorsal sometimes darkly spotted. Caudal dark on the proximal two-thirds, lighter distally. Anal yellowish with a faint sooty overlay, sometimes with ill-defined dark spots in the position of the ocelli in males. Pelvics hyaline, usually with a dusky overlay.

Ecology. Habitat. The species is apparently confined to sheltered or relatively undisturbed water, being common in bays and gulfs where the water is less than 40 ft. deep, and the bottom is of soft mud, sand or shingle. Available records suggest that the species favours a mud substrate.

Food. Of the 21 fishes examined (from 9 localities), only 6 contained food in the guts. In each case the food comprised fragmentary fish remains, unidentifiable except in one instance (a small *Haplochromis* species).

Breeding. All fishes less than 160 mm. S.L. are immature ; one larger individual (a female 163 mm. S.L.) is also immature. Males and females appear to reach the same maximum adult size.

Affinities. The very oblique mouth, marked prognacity, and relatively deep body (at least in adults) serve to distinguish *H. xenostoma* from the majority of larger *Haplochromis* species in the lake. There is some resemblance between this species and *H. macrognathus* and *H. plagiostoma,* both species with an oblique mouth, and in the case of *H. macrognathus,* a prominent lower jaw.

Haplochromis xenostoma is readily distinguished from *H. macrognathus* by its broader head (interorbital width 20·4–27·5, M = 24·5% head *cf.* 16·5–22·2, M = 18·6% ; snout 1·2–1·5 times as long as broad, *cf.* 1·5–2·2 times in *H. macrognathus*), and its more oblique mouth. The neurocranium also differs, that of *H. macrognathus* being of the "*prognathus*" type, whilst the skull of *H. xenostoma* is clearly of the "*serranus*" type (see p. 111 and discussion on pp. 109–113 ; also Greenwood, 1962).

From *H. plagiostoma, H. xenostoma* differs in its larger adult size, longer and narrower snout (34·2–39·2, M = 37·4% head, *cf.* 28·2–35·5, M = 32·5%), more prominent and longer lower jaw (50·0–62·0, M = 57·0% head, *cf.* 44·0–54·5, M = 49·2% ; lower jaw rarely projecting in *H. plagiostoma*) and the greater number of teeth in the outer row of the upper jaw (56–94, M = 82, *cf.* 44–68, M = 57). Neurocranial form in these two species is similar (see p. 113).

Another species with an oblique mouth is *H. cavifrons.* It is distinguished from *H. xenostoma* by its unique mottled coloration, lack of prognacity, broader snout (as long as broad or slightly broader than long, *cf.* 1·2–1·5 times as long as broad), and fewer teeth (56–74, M = 63, *cf.* 56–94, M = 82). The profile of the head also differs (compare fig. 6 above with fig. 20 in Greenwood, 1962).

Phylogenetically, *H. xenostoma* could be derived from a species resembling *H. plagiostoma*; its affinities seem to lie more with the "*serranus*" group than with the "*prognathus*" group to which *H. macrognathus* belongs. (See also discussion on pp. 113).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.257 (Paralectotype)	Entebbe	Degen
B.M. (N.H.) 1966.3.9.92–93	Napoleon Gulf, near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.88, 96–106	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.87	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.90–91	Off Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
	KENYA	
B.M. (N.H.) 1966.3.9.89	Naia Bay (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.86	Nanga Bay (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.9.9.85	Off mouth of Nzoia River	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1901.6.24.90 (Lectotype)	Locality unknown	Sir H. H. Johnston
B.M. (N.H.) 1966.3.9.94–95	Locality unknown	E.A.F.R.O.

Haplochromis pseudopellegrini sp. nov.

(Text-fig. 8)

HOLOTYPE: an adult male 139 mm. standard length, from Pilkington Bay (Uganda). B.M. (N.H.) no. 1966.2.21.2.

Named *pseudopellegrini* because of its resemblance to *H. pellegrini* Regan.

DESCRIPTION: based on 17 specimens (including the holotype) 98 to 150 mm. standard length.

Depth of body 29·0–33·5 (M = 30·9) per cent of standard length, length of head 32·4–37·0 (M = 33·8) per cent. Dorsal head profile gently curved (rarely straight) but interrupted by the prominent premaxillary pedicels.

Preorbital depth 19·1–22·4 (M = 20·4) per cent of head length, least interorbital width 20·4–27·1 (M = 23·9) per cent. Snout a little longer than broad (1·2–1·3 times), its length 35·1–39·0 (M = 37·1) per cent of head; eye diameter 18·5–25·4 (M = 20·6), depth of cheek 24·0–29·6 (M = 26·8) per cent.

Caudal peduncle 16·3–20·8 (M = 18·3) per cent of standard length, 1·3–2·0 (modal range 1·6–1·7) times as long as deep.

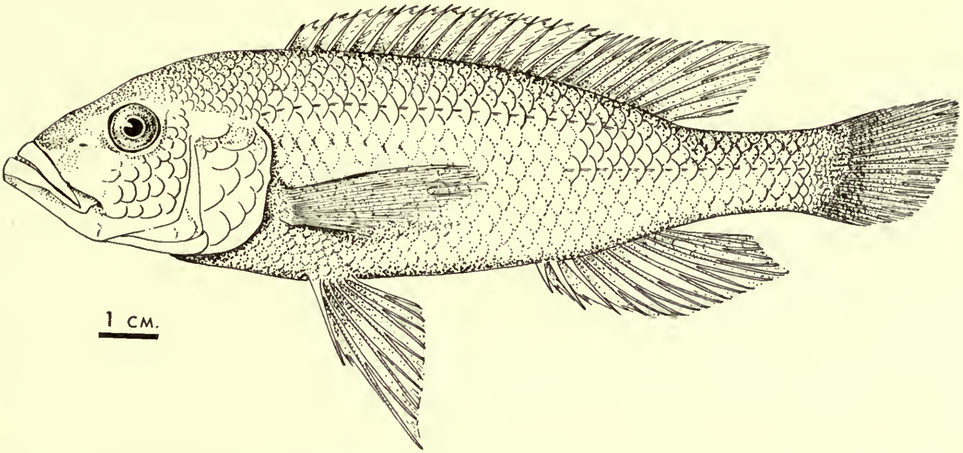

FIG. 8. *Haplochromis pseudopellegrini*; this specimen shows extreme development of an obliquely truncate caudal fin. Drawn by Barbara Williams.

Mouth slightly oblique, lower jaw projecting a little. Premaxilla slightly expanded medially. Lower jaw 46·8–53·4 (M = 49·1) per cent of head, 2·0–2·6 (modal range 2·1–2·4) times as long as broad. Posterior tip of the maxilla reaching, or almost reaching the vertical through the anterior orbital margin, extending a little beyond this point in a few specimens.

Gill rakers: of variable form, from relatively slender to moderately stout (reduced to short knobs in one specimen), the upper four sometimes flat; 9 (rarely 8 or 10) on the lower part of the first gill arch.

Scales: ctenoid; lateral line with 32 (f.4), 33 (f.7), 34 (f.4) or 35 (f.1) scales. Cheek with 4 (less commonly 3, rarely 5) rows. Six or 7 (rarely 7½) scales between the dorsal fin origin and the upper lateral line, 7 (occasionally 6, rarely 8) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.4) or 25 (f.12) rays, comprising 15 (f.9) or 16 (f.8) spinous and 8 (f.1), 9 (f.12) or 10 (f.4) branched rays. Anal with 11 (f.10) or 12 (f.7) rays, comprising 3 spines and 8 (f.10) or 9 (f.7) branched elements. Pectoral 22·7–28·0 (M = 24·9) per cent of standard length. First branched ray of pelvic fin slightly produced in both sexes, proportionately more so in adult males. Caudal scaled over its proximal half; in most specimens the fin is truncate or subtruncate but in a few the lower half, or the ventro-posterior corner, slopes obliquely forward and may also be rounded.

Teeth. The outer row of teeth in both jaws is composed of slender and slightly recurved unicuspids; there are 35–52 (M = 44) teeth in the outer row of the upper jaw.

Inner teeth are also unicuspid, and are implanted at an angle varying from near vertical to almost horizontal, the latter condition being most common. There are 2 (rarely 3) rows of inner teeth in the upper jaw, and 1 or 2 rows in the lower.

Osteology. The neurocranium of *H. pseudopellegrini* shows some similarity with that of *H. mento* and other species in the "*prognathus*" group (see Greenwood, 1962, and p. 110), but at the same time it retains characteristics of the more generalized skull seen in *H. serranus* and its allies. In this respect it resembles the neurocranium of *H. prognathus*, but is slightly less "*mento*"-like. In general appearance and proportions it is similar to the neurocrania of *H. bayoni* and *H. dentex* but lacks the characteristically decurved ethmo-vomerine region of these species (see Greenwood, *op. cit.*).

The premaxilla is moderately beaked, that is, the dentigerous part of the bone is somewhat expanded medially; the pedicels are short, being about two-thirds the length of the dentigerous arm.

The lower pharyngeal bone is triangular, its dental surface is as long as broad or slightly longer than broad. Lower pharyngeal teeth are slender and compressed, those in the two median rows are slightly coarser than their lateral congeners; the teeth are arranged in 22–24 rows. Vertebral counts in 14 specimens are: 13 + 17 (f.4), 13 + 18 (f.1), 14 + 17 (f.9), giving totals of 30 and 31.

Coloration: Live colours are known only for *adult and sexually active males*, which have the dorsal surface of the head and body dark brown, the flanks and belly golden-yellow overlain by an orange-red flush on the chest and anterior flanks, and also on the operculum. Dorsal fin dark neutral with a slight orange flush. Caudal dark neutral, with a reddish flush at the base and over the ventral quarter of the fin. Anal neutral, with yellowish-red ocelli. Pelvics are sooty.

Preserved material: Males (adult and active): ground colour brownish overlying silver, silvery-yellow on the chest and belly, and on the operculum; rest of head (including the branchiostegal membrane) brownish with very faint traces of a lachrymal blotch. Dorsal fin hyaline, with a faint, narrow black band running from the tip of the eleventh spine to about the middle of the last branched ray (*i.e.* curving gently downwards). Caudal brownish to hyaline, dark on the proximal half. Anal hyaline, with faint traces of one or two whiteish-grey ocelli. Pelvics sooty, darkest on the anterior half.

Adult but quiescent males are light brown dorsally, shading to silvery below, some showing a faint but broad and dark midlateral stripe, and a fainter upper lateral band above the upper lateral line. The two lateral bands are connected by 4–6 vertical bars, which extend ventrally a little below the midlateral band; where the lines intersect, the lateral one is diffusely expanded. A faint lachrymal blotch is present below the anterior part of the orbit. All fins are yellowish-brown, the soft dorsal and the proximal part of the caudal are often darkly maculate. Anal with 2 or 3 faint, whiteish ocelli. Pelvics variable, from yellowish-brown to sooty.

Ecology. Habitat. The species is recorded from four localities only. Two of these are shallow, sheltered bays, one is a fairly exposed, offshore and deep (90 ft.) channel, and the fourth is not fully documented except for a note that the nets were set in water about 20 ft. deep. In all, the substrate is of organic mud.

Food. Fourteen specimens were examined, and of these only two contained food, very fragmentary and generically unidentifiable fish remains.

Breeding. Little information is available on the reproductive biology of this species. The sex of the smallest specimen (98 mm. S.L.) is indeterminable; the others (132–153 mm.) are all adults, and only two are females. The two largest fishes are males.

Affinities. In general appearance *H. pseudopellegrini* closely resembles *H. pellegrini*; however, it reaches a much larger adult size, and the preserved coloration of adult males is much lighter (uniformly dark brown, nearly black in *H. pellegrini*, light brown over silver in *H. pseudopellegrini*). The species also differ in certain morphometric characters. *Haplochromis pseudopellegrini* has a longer snout (35·1–39·0, M = 37·1% head, *cf.* 30·8–36·0, M = 34·0%), a longer and more slender caudal peduncle (16·3–20·8, M = 18·3% standard length, *cf.* 13·2–17·8, M = 15·4%; length/depth ratio 1·3–2·0 [modal range 1·6–1·7], *cf.* 1·1–1·5 [mode 1·3]); unfortunately it is not possible to determine whether, at least in part, these differences are attributable to the larger size of the *H. pseudopellegrini* specimens. There are fairly marked interspecific differences in neurocranial form, and these do not appear to be influenced by size. The neurocranium in *H. pellegrini* shows much greater departure from the generalized condition than does that of *H. pseudopellegrini* (for *H. pellegrini*, see Greenwood, 1962).

In its general facies, *H. pseudopellegrini* resembles *H. guiarti*, *H. altigenis*, *H. dentex*, *H. mento* and *H. gowersi*, particularly the former species.

The differences separating *H. pseudopellegrini* from *H. altigenis* are discussed on p. 64; *H. pseudopellegrini* could represent the ancestral morphotype from which *H. altigenis* evolved.

From *H. guiarti* it is distinguished by its different neurocranial form, and the following: slightly longer snout (35·1–39·0, M = 37·1% head, *cf.* 31·7–37·5, M = 34·4%), slightly narrower interorbital region (20·4–27·1, M = 23·9% head, *cf.* 23·4–30·2, M = 27·4%), longer and narrower lower jaw (48·6–53·4, M = 49·1% head, *cf.* 39·2–48·2, M = 44·4%; length/breadth ratios 2·0–2·6 [modal range 2·1–2·4] *cf.* 1·5–2·3 [mode 2·0]), fewer teeth in the outer row of the upper jaw (35–52, M = 44, *cf.* 48–74, M = 62).

From *H. gowersi* it differs in head shape (and neurocranial form), and in having a much shorter head (34·2–37·0, M = 33·8% standard length, *cf.* 35·8–38·4, M = 37·0%), a broader snout, a larger eye (18·5–23·4, M = 20·6% head, *cf.* 15·5–19·3, M = 17·5%), a slightly shallower cheek (24·0–29·6, M = 26·8% head, *cf.* 27·8–33·3, M = 29·5%), and a longer caudal peduncle (16·3–20·8, M = 18·3% standard length, *cf.* 13·3–17·6, M = 14·8%).

From *H. dentex*, *H. pseudopellegrini* differs, superficially, by its less strongly decurved dorsal head profile. At a deeper level, there are differences in the shape of the neurocranium, that of *H. dentex* having a sharply decurved ethmoid-vomer region (see Greenwood [1962], p. 168 and fig. 25); but in other respects, the neurocrania of the two species are similar. Other interspecific differences lie in the more numerous and closely set teeth of *H. pseudopellegrini* (35–52, M = 44, *cf.* 32–48, M = 36), its deeper body (29·0–33·5, M = 30·9% of standard length, *cf.* 24·6–29·5, M = 26·7), and the greater posterior extension of the maxilla in this species (posterior maxillary tip reaching anterior orbital margin or to below the eye, *cf.* not reaching the orbital margin).

From *H. estor*, *H. pseudopellegrini* differs, principally, in having a shorter head

(32·4–37·0, M = 33·8% standard length, *cf.* 37·2–38·5, M = 37·8%), a shorter lower jaw (46·8–53·4, M = 49·1% head, *cf.* 54·2–57·5, M = 55·5%), and a longer caudal peduncle (16·3–20·8, M = 18·3% standard length, *cf.* 14·3–16·1, M = 15·8%). Neurocranial form in the two species differs, that of *H. estor* belonging to the "*prognathus*" group, whilst that of *H. pseudopellegrini* has stronger affinities with the "*altigenis*"-type (see p. 110).

The resemblance between *H. pseudopellegrini* and *H. mento* is probably the most distant of all. Osteologically, there is a clear-cut difference in neurocranial form (like that distinguishing *H. pseudopellegrini* and *H. estor*), and in most specimens the external head shape is distinctive (*cf.* fig. 12 in Greenwood [1962] with Text-fig. 8 above). Nevertheless, most cephalic morphometric characters are similar in the two species, although the snout of *H. pseudopellegrini* is broader (length/breadth ratio 1·1–1·3 *cf.* 1·5–1·8 in *H. mento*). The outer teeth in *H. mento* are stouter and more strongly curved than those of *H. pseudopellegrini*; the range for the number of outer upper jaw teeth overlaps in the two species, but the mean for *H. pseudopellegrini* is lower (44 *cf.* 52).

Phyletically, *H. pseudopellegrini* appears to be a derivative from an *H. guiarti*-like stem, and thus shows relationship with *H. bayoni* and *H. dentex*. However, unlike these species it also shows relationship with both *H. altigenis* and *H. pellegrini*. Structurally, *H. pseudopellegrini* could represent an ancestral level in the evolution of *H. altigenis*.

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.299–310	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.296	Trawl in Buvuma Channel off Nasu Point	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.297	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.2 (Holotype)	Pilkington Bay . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.298	Sesse Islands	E.A.F.R.O.

Haplochromis altigenis Regan, 1922

(Text-figs. 9 and 10)

Paratilapia longirostris (part): Boulenger, *Cat. Afr. Fish.*, **3**, 332.
Pelmatochromis spekii (part): Boulenger, 1915, *op. cit.*, *tom. cit.*, 417.
Haplochromis altigenis Regan, 1922, *Proc. zool. Soc. Londn.*, 175, Pl. 1.

LECTOTYPE: a male, 186 mm. standard length from Bunjako (Uganda), collected by Degen. B.M. (N.H.) reg. no. 1906.5.30.294.

DESCRIPTION: based on 25 specimens (including the lectotype and paralectotype), 100–202 mm. standard length.

Depth of body 28·4–34·7 (M = 31·5) per cent of standard length, length of head 36·7–39·5 (M = 38·2) per cent. Dorsal head profile gently curved, rather variable in its shape, tending to slope more steeply in large fishes which therefore have more rounded profiles; the two type specimens have the most strongly sloping head

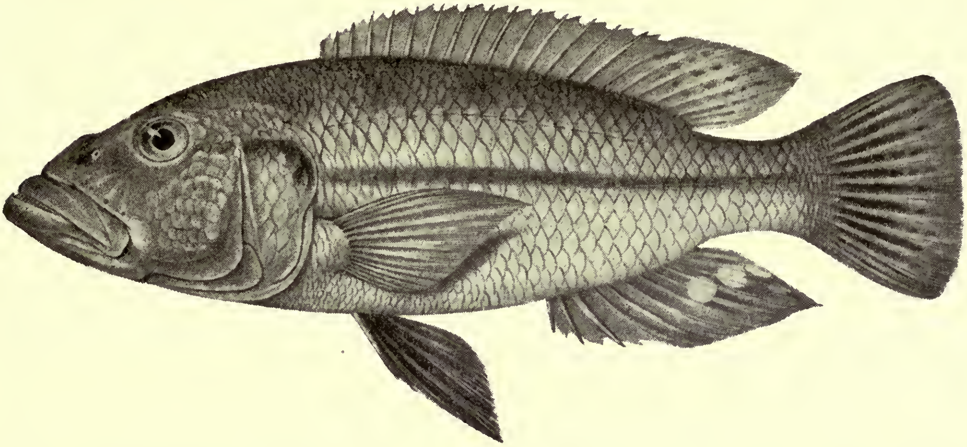

FIG. 9. *Haplochromis altigenis*; lectotype, about ·57 times natural size. From Regan, *Proc. zool. Soc.*

profiles (*ca* 40°); most other specimens lie in the range 30°–35°. The premaxillary pedicels are prominent, and clearly break the outline of the profile. Altogether, one is left with the impression of a heavy-headed fish.

Preorbital depth 17·6–23·7 (M = 19·9) per cent of head length, least interorbital width 17·4–25·0 (M = 20·2) per cent. Snout 1·1–1·3 times as long as broad, its length 36·6–42·2 (M = 39·3) per cent of head, eye diameter 16·9–21·7 (M = 19·2), depth of cheek 25·6–34·5 (M = 30·5) per cent. Cheek depth may show positive allometry with standard length in fishes > 180 mm.; the three largest fishes have the deepest cheeks.

Caudal peduncle 12·4–16·0 (M = 14·7) per cent of standard length, 1·2–1·4 (mode 1·3) times as long as deep.

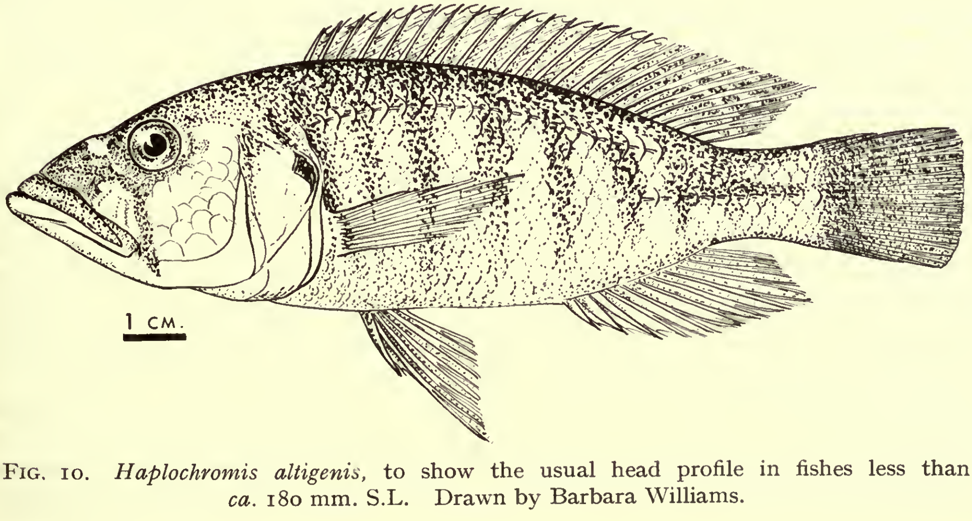

FIG. 10. *Haplochromis altigenis*, to show the usual head profile in fishes less than *ca.* 180 mm. S.L. Drawn by Barbara Williams.

Mouth slope variable, from near horizontal to moderately oblique (20°–30°). Lips slightly thickened, the premaxilla expanded medially. Lower jaw generally projecting (but jaws equal anteriorly in some specimens), its length 51·0–55·8 (M = 52·7) per cent of head, 1·8–2·4 (modal range 1·9–2·0) times as long as broad. Posterior tip of the maxilla almost reaching the vertical through the anterior orbital margin (reaching this point in a few specimens).

Gill rakers : stout (finer in the two smallest fishes), the upper 1–4 sometimes flattened and anvil-shaped ; 8 or 9 (rarely 7 or 10) on the lower part of the first arch.

Scales : ctenoid ; lateral line with 31 (f.7), 32 (f.13) or 33 (f.4), cheek with 4–6 (mode 5) rows. Six to 8 scales between the upper lateral line and the dorsal fin origin ; chest and anterior belly scales small, 7 or 8 (rarely 9) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.8), 25 (f.16) or 26 (f.1) rays, comprising 15 (f.22) or 16 (f.3) spinous and 9 (f.10) or 10 (f.15) branched rays. Anal with 11 (f.2), 12 (f.22) or 13 (f.1) rays, comprising 3 spines and 8 (f.2), 9 (f.22) or 10 (f.1) branched elements. Pectoral 20·1–26·2 (M = 22·6) per cent of standard length. Pelvics with the first branched ray produced, usually more so in males but almost as elongate in some females. Caudal subtruncate, scaled on its proximal half.

Teeth. In the size range of fishes studied, all teeth in the outer row of both jaws are stout, unicuspid and curved. There are 40–60 (M = 50) teeth in the outer row of the upper jaw.

The inner teeth of the two smallest fishes (90 and 119 mm. S.L.) are predominantly unicuspids, but some weakly tricuspid teeth occur in both jaws. In all other specimens, only unicuspids are found ; these are moderately large, curved and implanted obliquely. The inner tooth rows are often irregularly arranged, with 3 (rarely 4) rows in the upper jaw, and 2 or 3 in the lower.

Osteology. The neurocranium of *H. altigenis* resembles that of *H. bayoni*, but is relatively broader in the otic region. Thus, although it shows some of the characters associated with the *H. mento*-type skull (see Greenwood, [1962], fig. 25) it still retains the curved preorbital profile, greater preorbital skull depth, and broad otic region of the more generalized neurocranium. In these characters it also resembles the neurocranium of *H. pseudopellegrini*.

The dentary and premaxillary show no outstanding characters. The former is a stout bone, and the dentigerous surface of the latter is but moderately expanded medially (less so, for example, than in *H. bayoni*).

The dentigerous surface of the lower pharyngeal bone is as broad as long but is broader than long in large fishes. Anteriorly this surface narrows rather abruptly so that the apex of the dentigerous triangle is produced into a narrow " stem ". The lower pharyngeal teeth are rather coarse, somewhat compressed and clearly but weakly cuspidate.

Vertebral counts in 7 specimens are : 13 + 16 (f.5) and 13 + 17 (f.2), giving totals of 29 and 30.

Coloration. Live colours are unknown. *Preserved material : Males* (*adult and sexually active*)*:* ground coloration a very dark brown, almost black on the dorsal surface and snout, and with a sooty overlay on the chest. Lower jaw and branchiostegal membrane pinkish-brown ; margin of the preoperculum outlined in dark brown. Dorsal fin yellow-brown, lappets black, and with a faint black outline to the margin of the soft part. Caudal darker yellow-brown (darkest proximally). Anal yellow-brown, with 2 large, dead-white ocelli. Pelvics very dark brown, appearing black when folded. Pectorals dark brown (dark pectorals are unusual).

Males (*adult but sexually quiescent*) have a light brown ground coloration, darker on the dorsal surface of the snout, head and body. A prominent, but narrow, dark lachrymal stripe runs from the lower anterior border of the eye, passes almost vertically downwards behind the posterior tip of the maxilla to end on the dentary ; a slightly broader dark bar lies immediately anterior to the vertical limb of the preoperculum. The lower jaw and branchiostegal membrane are very light brown ; the chest is somewhat dusky. The flanks and caudal peduncle are crossed by seven very faint, moderately broad dark bars ; these extend (on the flanks) from the dorsal fin base almost to the ventral body outline. Dorsal fin yellow-brown, the lappets black and the soft part darkly maculate. Caudal yellowish-brown, darkest on the proximal half. Anal dark yellow-brown. Pelvics dark brown, nearly black, on the anterior half, otherwise light yellow-brown.

Male (*immature*) : essentially as for females (see below), but with black lappets on the dorsal fin, the caudal uniformly light but with some dark spots on the upper fifth, 3 faint whiteish ocelli on the anal, and a dusky overlay on the pelvics.

Note on the coloration of the type specimens. Both these specimens are males, but both are now a pale silver, shading to white. One specimen (that illustrated by Regan, see fig. 9 above) has a very faint midlateral stripe, which is now much fainter than is shown in the figure. Both fishes have dusky pelvics. In one, there are five, large, dead-white ocelli (arranged in three rows) on the anal fin, and in the other there are four (in two rows). The difference in coloration between these specimens and those described above is, presumably, due both to time and to the fact that the types were not fixed in formol but in alcohol.

Females (*immature and adult*) : ground coloration light brown, darkest dorsally, and shading to yellowish-silver on the chest and belly. Lachrymal and preopercular stripes are as described for males, but in addition there are two, faint, parallel dark bands across the snout. The lower jaw and branchiostegal membrane are light yellow-brown. A faint dark midlateral band runs along the flank from slightly behind the opercular margin to the base of the caudal fin (sometimes extending onto the fin itself), and is crossed by 8 to 10, moderately broad vertical bars which extend from the dorsal fin base to about the level of the pectoral fin. Dorsal fin light greenish-brown, the soft part darkly maculate. Caudal yellow-brown on its distal quarter to third, dark brown basally. Anal greenish-brown. Pelvics light yellow-brown, somewhat darker along the anterior margin.

Three fishes (140, 148 and 149 mm. S.L.) caught on two occasions off Kisigala; Point, North Kome Island, show typical piebald coloration of black on silver ; all three are immature females. These are the first known examples of piebald polychromatism amongst the piscivorous species-groups of Lake Victoria *Haplochromis*, although the phenomenon is recorded from other trophic and phyletic lines (see Greenwood, 1956, 1957, 1959, and p. 95 below).

Ecology. Habitat. The species occurs over both hard and soft substrates in sheltered bays and gulfs, as well as off-shore in places where the water is relatively undisturbed; apparently it does not occur at depths of over 50 ft.

Food. Eleven of the 26 specimens examined (from 15 localities) contained food in the gut. In all cases this consisted of finely macerated fish remains, identifiable as cichlids in three specimens, and as *Haplochromis* species in six others.

Breeding. Haplochromis altigenis is a female mouth breeder. Fishes less than 145 mm. S.L. are immature, or, in the upper levels of the range, show early signs of maturation. The largest specimen (202 mm. S.L.) is a female, but both sexes occur in the size range 170–194 mm.

Affinities. At least superficially, four species, *H. pseudopellegrini*, *H. estor*, *H. dichrourus* and *H. gowersi*, closely resemble *H. altigenis*. A fifth species, *H. squamulatus* shows a more distant resemblance.

Similarities between *H. altigenis* and *H. dichrourus* are considered elsewhere (see p. 68); the resemblances between these species may indicate a fairly close phyletic relationship.

From *H. pseudopellegrini*, *H. altigenis* is distinguished by its longer head (36·7–39·5, M = 37·2% of standard length, *cf.* 32·4–37·0, M = 33·8%), deeper cheek (25·6–34·5, M = 30·5% head, *cf.* 24·0–29·0, M = 26·8%), longer lower jaw (51·0–55·8, M = 52·7% head, *cf.* 46·8–53·4, M = 49·1%) and its shorter and deeper caudal peduncle (12·4–16·0, M = 14·7% standard length, *cf.* 16·3–20·8, M = 18·3%, length/depth ratio 1·2–1·4 [mode 1·3] *cf.* 1·3–2·0 [modal range 1·6–1·7]). The neurocranium in the two species is generally similar. It seems that *H. altigenis* could have evolved from an *H. pseudopellegrini*-like ancestor.

From *H. estor*, *H. altigenis* differs in its longer snout (36·6–42·2, M = 39·3% head, *cf.* 34·5–37·0, M = 36·2%), smaller eye (16·9–21·7, M = 19·2% head, *cf.* 22·8–25·4, M = 24·5%), much deeper cheek (25·6–34·5, M = 30·5% head, *cf.* 22·8–25·4, M = 24·5%) and slightly shorter lower jaw (51·0–55·8, M = 52·7% head, *cf.* 54·2–57·5, M = 55·5%). There are fairly marked differences between the neurocrania of the two species, that of *H. estor* being of the "*prognathus*" type.

Superficially, the resemblances between *H. gowersi* and *H. altigenis* are great, and some difficulty may be experienced in separating certain specimens of the two species. However, there are distinct differences between modal specimens of the two species, and there is a clear difference in neurocranial form; the skull of *H. gowersi* is of the "*prognathus*" type. This difference in neurocranial shape probably accounts for the more declivous snout and dorsal head profile of *H. altigenis*, and the greater prominence of the premaxillary pedicels in this species. In addition to these qualitative differences, *H. altigenis* differs from *H. gowersi* in having the interorbital width equal to or slightly greater than the preorbital depth (interorbital less than preorbital in *H. gowersi*), a broader head (greatest width, measured at about the middle of the operculum, 41·5–45·5, M = 42·7% head, *cf.* 35·6–39·0, M = 36·8); the greater head breadth is also reflected in the broader lower jaw of *H. altigenis*.

Haplochromis squamulatus and *H. altigenis* both have noticeably rounded head profiles, and very small chest and anterior belly scales. However, they differ in several morphometric characters. *Haplochromis altigenis* has a longer head, narrower interorbital, longer snout, deeper cheek and a longer lower jaw (see p. 87). The neurocrania show several interspecific differences (that of *H. squamulatus* showing affinities with the neurocrania of *H. martini* and *H. michaeli*) and there are marked differences in preserved coloration.

Considering the evidence available, both morphometric and osteological, it seems *H. altigenis* could have evolved from an *H. pseudopellegrini*-like stem ; certainly its neurocranial form does not favour a closer association with *H. estor* and *H. gowersi* than with *H. pseudopellegrini*.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.294 (Lectotype)	Bunjako	Degen
B.M. (N.H.) 1906.5.30.295 (Paralectotype)	Bunjako	Degen
B.M. (N.H.) 1966.3.9.220–227	Napoleon Gulf, near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.228–235	Karenia Beach, near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.215–216	Near Ramafuta Island (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.219	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.218	Manadu Island	E.A.F.R.O.
B.M. (N.H) 1966.3.9.213–214	Off Entebbe harbour . . .	E.A.F.R.O.
	TANZANIA	
B.M. (N.H.) 1966.3.9.217	Mwanza Harbour . . .	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.211–212	Locality unknown . . .	E.A.F.R.O.

Haplochromis dichrourus Regan, 1922

(Text-fig. 11)

Paratilapia serranus (part) : Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 334.
Haplochromis dichrourus Regan, 1922, *Proc. zool. Soc. Londn.*, 178, fig. 6.

HOLOTYPE : a juvenile female, 113·0 mm. S.L., from Buganga ; B.M. (N.H.) reg. no. 1906.5.30.265.

DESCRIPTION : based on eight specimens (including the holotype), 84–186 mm. S.L.

Depth of body 28·6–35·5 (M = 32·1) per cent of standard length, length of head 35·2–37·7 (M = 36·6) per cent. Dorsal head profile convex, sloping steeply (*ca* 40°) especially in the snout region ; premaxillary pedicels prominent and breaking the outline of the profile.

Preorbital depth 16·4–21·0 (M = 18·7) per cent of head, least interorbital width 18·0–24·6 (M = 21·3) per cent. Snout 1·10–1·25 times as long as broad, its length

34·1–41·0 (M = 37·4) per cent of head, eye diameter 19·4–24·6 (M = 21·1), depth of cheek 23·0–30·6 (M = 27·6) per cent.

Caudal peduncle 12·4–17·2 (M = 15·2) per cent of standard length, 1·1–1·5 times as long as deep.

Mouth slightly oblique (20°–30°), lips thickened, premaxilla slightly expanded medially. Lower jaw projecting, its length 49·0–54·0 (M = 52·7) per cent of head, 1·8–2·6 (no distinct mode) times as long as broad. Posterior tip of maxilla reaching the vertical through the anterior margin of the orbit, or to below the anterior part of the eye.

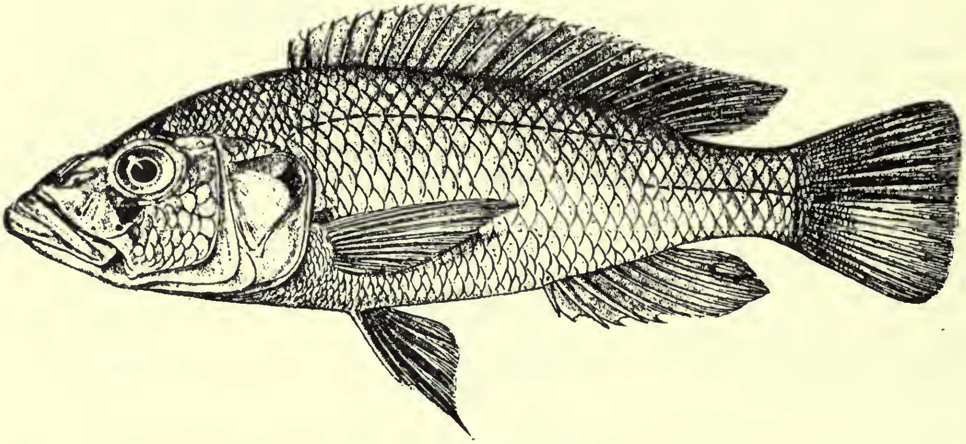

FIG. 11. *Haplochromis dichrourus*; holotype, about ·93 times natural size. From Regan, *Proc. zool. Soc.*

Gill rakers: stout, the lower 2 or 3 reduced, the upper 3 or 4 flat and expanded in some specimens; 8 or 9 (mode) on the lower part of the first gill arch.

Scales: ctenoid; lateral line with 32 (f.2), 33 (f.4) or 34 (f.2), cheek with 3 (f.1), 4 (f.1), 5 (f.5), or 6 (f.1) rows. Seven to 9 scales between the upper lateral line and the dorsal fin origin, 6–9 (mode 8) between the pectoral and pelvic fin bases; scales on the chest and belly small.

Fins: Dorsal with 25 rays, comprising 15 (f.1) or 16 (f.7) spinous and 9 (f.7) or 10 (f.1) branched rays. Anal with 11 (f.2), 12 (f.5) or 13 (f.1) rays, comprising 3 spines and 8 (f.2), 9 (f.5) or 10 (f.1) branched elements. Pectoral fin 21·2–27·3 (M = 23·7) per cent of standard length. Pelvics with the first, and to a lesser degree, the second branched rays produced, slightly so in females and markedly elongate in males. Caudal truncate or subtruncate.

Teeth. In all specimens the outer teeth (numbering 48–70, M = 58 in the upper jaw) are unicuspid, slender and very strongly curved (the tips of the anterolateral premaxillary teeth are not visible when the specimen is viewed laterally).

The inner teeth in fishes > 149 mm. S.L. are all unicuspid, curved and obliquely implanted. In the four smaller specimens, the 113 mm. fish (holotype) has mostly tricuspids in the upper jaw and an admixture of tri- and unicuspids (the latter predominating) in the lower jaw ; the 84, 101 and 121 mm. specimens have a mixture of unicuspids and weakly bicuspids in both jaws ; as in the larger fishes, these teeth are curved and obliquely implanted. The inner teeth are arranged in 1–3 series in the upper jaw, and in 2 or 3 in the lower (in a single row in one fish).

Osteology. With so few specimens available, it has not been possible to prepare a complete skeleton, but radiographs have been studied.

The lower pharyngeal bone is fine, with a triangular dentigerous surface which is equilateral or slightly broader than long. The lower pharyngeal teeth are slender, with cylindrical necks and slightly compressed weakly cuspidate crowns, and are arranged in 20–22 rows. Vertebral counts in 5 specimens are : 13 + 16 (f.1) and 13 + 17 (f. 4), giving totals of 29 and 30.

Ecology. Habitat. The species has a wide depth range, from 10–90 feet. It is found in both sheltered and exposed places (including beaches) over sand and shingle substrata.

Food. Of the five specimens examined (from four localities) four contained food in the gut. In three fishes this consisted solely of fish remains (*Haplochromis* sp.), and in the fourth fish-remains (a cichlid) and fragments of larval insects (one probably a dragon-fly, the other Ephemeroptera).

Breeding. Little information is available ; three of the smallest fishes (101, 113 and 121 mm. S.L.) are immature females.

An unusual feature of this species is the coloration of females, which, at least in preserved specimens, seems to be as polychromatic as that of males, and certainly more complex than the female coloration of other species (except, perhaps, *H. chromogynos*).

Coloration. The only information on live colours is provided by brief field notes made on a sexually active male caught in deep water near Soswa island. In this fish the median fins and back were described (by Mr. J. D. Kelsall) as vivid flame red, the belly as jet black.

Preserved Colours : Males. The most extreme pattern is shown by a fish which, although adult, is in an early stage of sexual activity. The upper part of the head (above the level of the lower orbital rim) brownish, snout yellowish and crossed by a thin, well-defined and dusky bar ; running parallel with the premaxillary pedicels are a pair of short, dark bars, each of which (at about the level of the pedicel tips) broadens somewhat and curves sharply at right angles to meet the orbit. The lower part of the head (cheeks, preorbital and the entire operculum) jet black. This colour extends onto the chest but does not reach above the level of the pectoral fin base. Immediately behind the pectoral fin, the margin of this black area curves ventrally but rises again above the vent so that the posterior half of the body is black on its lower half. On the caudal peduncle the dark area rises again to cover about the entire lateral aspect. Above the black areas the body is brownish. Dorsal and caudal fins are dark yellow-orange, with a narrow black crescent at the caudal base. The anal fin is a similar colour, with two ocelli, each outlined by a narrow black margin. Pelvics jet black, except for the yellowish innermost ray of each side.

In two other males (both sexually active, with convoluted testes and therefore thought to be more mature than the specimen above) the head and anterior half of the body are light orange-brown the posterior half and the caudal peduncle dusky brown. A well-defined black band crosses the snout (just above the upper lip) to the anterior margin of the preorbital bone. Another transverse black band at the level of the pedicel tips, runs from orbit to orbit. An interrupted band extends from the upper posterior margin of the orbit across the nape. A dusky, nearly vertical lachrymal stripe is present. The branchiostegal membrane and chest are black, but the belly is brown. Dorsal fin yellowish, the soft part is maculate, the spots being clear. Anal yellowish but dusky along its base, and with two, hyaline ocelli (set, in one specimen, in the dark basal zone). Caudal yellowish-grey, but with a broad, dusky band at its base. The pelvics are black except for the distal half of the membrane between the last two rays.

Females (*adult and immature*) *:* body and head dark grey-brown with a blueish hue. Branchiostegal membrane and chest dusky as are the lower parts of the operculum, preoperculum and interoperculum. Faint traces of snout and lachrymal bands (like those of males) are visible, as is a nuchal bar. Dorsal fin greyish to light sooty, the lappets dark. Anal pale orange with a single, well-defined, dead-white ocellus. Caudal with a dark base, the upper half grey and the lower orange. Pelvics light sooty, the pigment most concentrated on the anterior half of the fin.

Affinities. The anomalous coloration of female *H. dichrourus* was commented upon above. Apart from the relatively infrequent piebald females in certain species, and the occurrence of a piebald coloration as the usual one in females of *H. chromogynos* (see Greenwood, 1959), I know of no other species in Lake Victoria with colourful females.

In its gross morphology, *H. dichrourus* closely resembles *H. altigenis* although there are marked differences in the preserved coloration of the females. Both species have very small chest scales. They differ in that the maxilla of *H. dichrourus* reaches further posteriorly (rarely reaching the orbit in *H. altigenis*) and the premaxilla is not markedly expanded medially. Also, the teeth in *H. dichrourus* are more strongly curved, so that when viewed laterally, their tips are hidden ; in *H. altigenis*, the tips can always be seen.

The two smallest fishes resemble specimens of *H. pellegrini* of a similar size. They are, however, distinguished by their more slender and much more strongly recurved outer jaw teeth (in *H. pellegrini* these teeth have a gentle curvature confined to the distal part), and by having the maxilla extending further posteriorly (to below the anterior orbital margin). Also, in *H. dichrourus* the premaxillary pedicels are more prominent, and there are differences in preserved coloration.

Phyletically, *H. dichrourus* could be related to *H. altigenis* and *H. pellegrini*.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.265 (type)	Buganga	Degen
B.M. (N.H.) 1966.3.9.186	Jinja, off golf course . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.187	Katebo	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.188–9	Karenia, Napoleon Gulf . .	E.A.F.R.O.

	TANZANIA	
B.M. (N.H.) 1966.3.9.185	Off Soswa Island . . .	J. D. Kelsall
B.M. (N.H.) 1966.3.9.183–4	Beach N. of Majita . . .	E.A.F.R.O.

Haplochromis paraguiarti sp. nov.

(Text-fig. 12)

HOLOTYPE: an adult male 130 mm. standard length, from a beach near Nasu Point, Buvuma Channel (Uganda); B.M. (N.H.) reg. no. 1966.2.21.6.

Named *paraguiarti* because of its close superficial resemblance to *H. guiarti*.

DESCRIPTION: Based on 31 specimens (including the holotype), 70–156 mm. standard length.

Depth of body 31·7–36·6 (M = 34·1) per cent of standard length, length of head 33·0–36·8 (M = 34·8) per cent. Dorsal head profile straight or very slightly curved, the premaxillary pedicels forming a slight prominence.

Preorbital depth 14·5–19·5 (M = 16·9) per cent of head length, least interorbital width 22·9–27·7 (M = 25·3) per cent. Snout as long as broad or slightly longer (1·2 times), its length 31·0–36·2 (M = 33·5) per cent of head, eye diameter 23·8–28·6 (M = 26·2), depth of cheek 20·0–26·1 (M = 23·8) per cent.

Caudal peduncle 14·7–18·6 (M = 16·6) per cent of standard length, 1·3–1·9 (modal range 1·3–1·5) times as long as deep.

Mouth horizontal or slightly oblique, the jaws equal anteriorly. Lower jaw 41·0–48·6 (M = 45·0) per cent of head, 1·7–2·4 (modal range 1·9–2·1) times as long as broad. Posterior tip of the maxilla reaching the vertical through the anterior orbital margin, occasionally extending to below the eye. Premaxilla slightly expanded medially.

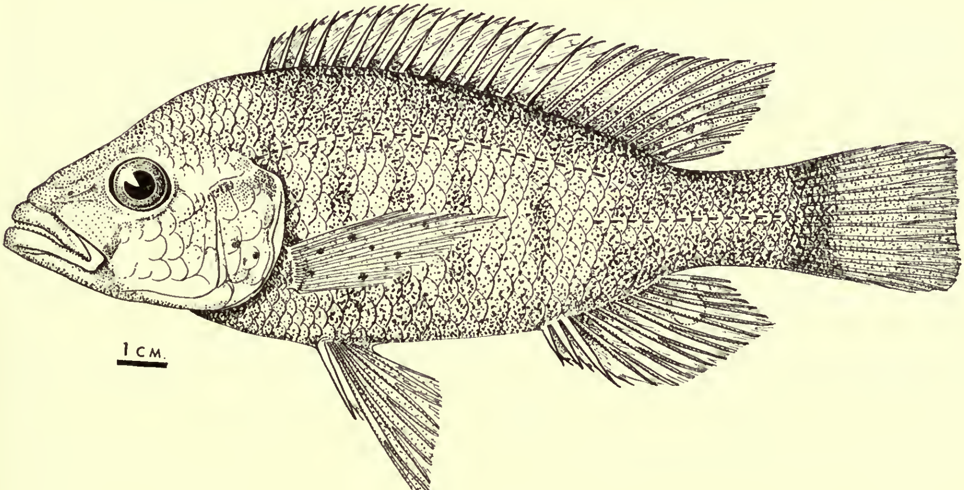

FIG. 12. *Haplochromis paraguiarti.* Drawn by Barbara Williams.

Gill rakers : moderately stout (relatively slender in fishes less than 90 mm. S.L.), the upper 4–6 flat and sometimes branched in fishes over 115 mm. S.L., the lower 1 or 2 reduced ; 8–10 (mode 9), rarely 11, on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 31 (f.4), 32 (f.12), 33 (f.12) or 34 (f.3) scales, cheek with 3 or 4 (rarely 2 or 5) rows. Five or 6 (rarely 6½) scales between the upper lateral line and the dorsal fin origin, 6 or 7 between the pectoral and pelvic fin bases. (Because many specimens were damaged during capture by gill-nets, the last two counts are based on only 17 specimens).

Fins : Dorsal with 23 (f.1), 24 (f.8), 25 (f.19) or 26 (f.3) rays, comprising 15 (f.21) or 16 (f.10) spinous and 8 (f.1), 9 (f.15) or 10 (f.15) branched rays. Anal with 11 (f.6), 12 (f.23) or 13 (f.2) rays, comprising 3 spines and 8 (f.6), 9 (f.23) or 10 (f.2) branched elements. Pelvic fins with the first unbranched ray slightly produced in the adults of both sexes, but proportionately more so in males. Pectoral 24·3–30·0 (M=26·3) per cent of standard length. Caudal truncate or subtruncate, scaled on its basal half to two-thirds.

Teeth : The form of the teeth in the outer row of both jaws shows some correlation with standard length. Only bicuspids (with a few tricuspids posterolaterally in the upper jaw) are found in fishes 70–75 mm. S.L. Unicuspids anteriorly, with bicuspids laterally are characteristic of most fishes 84–113 mm. S.L. (and in one exceptional individual 144 mm. S.L.). In most specimens over 112 mm. S.L., only unicuspids occur, but this is also the condition in a few fishes between 99 and 112 mm. S.L. The unicuspids are moderately stout teeth, and are only slightly curved. There are 42–62 (M = 54) outer teeth in the upper jaw.

Teeth in the inner rows are relatively large ; tricuspids predominate in fishes of all sizes, but in specimens over 120 mm. S.L. weakly tricuspids are commoner than the distinctly tricuspid ones, and some unicuspid teeth also occur (especially in the outermost row of the inner series). There are 3 or 4 inner rows in the upper jaw, and 2 or 3 (less frequently 1 row) in the lower.

Osteology : The neurocranium of *H. paraguiarti* is identical with that of *H. acidens* (see p. 75). It differs somewhat from the presumed generalized piscivore skull of *H. guiarti*, and shows some of the characters found in the more specialized type of *H. prognathus*. It is, in fact, almost intermediate between the two types.

The premaxilla has a less pronounced medial expansion than in *H. acidens*, but as in that species it has long pedicels (as long as the horizontal dentigerous arms) which meet the horizontal arms at an appreciable angle. In these characters the premaxilla of *H. acidens* differs from that bone in the generalized species like *H. guiarti* and *H. serranus*.

The lower pharyngeal bone is slender, its dentigerous surface slightly broader than long. The teeth are fine, slender, compressed and clearly bicuspid, only those in the posterior one or two rows of the median series are enlarged. There are 26–30 (mode 28) rows of lower pharyneal teeth.

Vertebral counts for 6 specimens are : 13 + 17 (f.4) and 14 + 16 (f.2), giving a total of 30.

Coloration : live colours unknown. *Preserved material : Males* (*adult and sexually active*) *:* ground colour dark sooty, almost uniformly so except for a lighter (dusky gold) patch on the midflank, crossed by four, faint and narrow vertical stripes. Branchiostegal membrane dark (darker below the opercular series than between the jaws). A very faint, near vertical lachrymal stripe runs from the anterior orbital margin to behind the posterior tip of the maxilla. Dorsal fin dusky, lappets black, the soft dorsal maculate. Caudal dark. Anal dusky, but lighter than the dorsal except for a narrow band along the base, and over the spinous part; two or three greyish ocelli present. Pelvics dusky, the proximal threequarters almost black, the distal quarter lighter.

Males (*adult but quiescent*) *:* ground colour dusky silver-grey, darkest dorsally; cheek bright silver. A faint lachrymal stripe present. Dorsal fin greyish-dusky, darkly maculate between the last four spines and all the branched rays. Caudal dark. Anal dark hyaline, with two or three greyish ocelli. Pelvics sooty, darkest on the leading edge.

Females (*adult*) *:* ground colour silver grey, darker dorsally: cheek bright silver (*i.e.* like quiet males but lighter and brighter). Dorsal fin dark hyaline, with dark spots on the soft part. Caudal dark hyaline, weakly to distinctly maculate. Anal and pelvic fins hyaline.

Females (*juvenile*) *:* Two small (75 mm. S.L.) specimens have colours like those of adult females, but with traces of 7 or 8 vertical bars on the flanks and caudal peduncle; these bars reach the dorsal outline but do not extend ventrally below the level of the pectoral fin base.

Ecology. Habitat. Most records of *H. paraguiarti* are from exposed, wave-washed beaches where the substrate is of sand, rock or shingle. There are, however, a few records from more sheltered beaches and areas, but with one exception (a mud bottom) the substrate was hard, and the depth invariably never more than 30 ft.

Food. Twenty specimens (from 12 localities) were examined. Of these, 17 contained ingested material. One individual contained fish remains (very fragmentary and unidentifiable, even to family) together with a little macerated phanerogam. tissue. Eleven others yielded either macerated plant tissue (f.4), or a mixture of plant tissue and insect fragments (larval Ephemeroptera); five specimens contained only fragments of larval Ephemeroptera.

Breeding. Little information is available on reproduction in this species. Fishes less than 95 mm. S.L. are immature, as is one larger specimen (a male, 100 mm. S.L.). The largest fish (156 mm. S.L.) is a male.

Affinities. Superficially, *H. paraguiarti* resembles *H. guiarti* both morphologically and trophically, although *H. guiarti* apparently includes a greater proportion of fish in its diet. Morphologically the species may be distinguished by the straight dorsal head profile of *H. paraguiarti* (gently curved in *H. guiarti*), its longer head (33·0–36·8, M = 34·8 per cent standard length *cf.* 29·5–33·8, M = 31·4 per cent), somewhat broader snout, and fewer, coarser outer teeth (42–60, M = 53, *cf.* 48–74, M = 62 is the upper jaw). Live colours are unknown for *H. paraguiarti*, but the coloration of preserved, sexually active males is noticeably darker than that of *H. guiarti* males. Osteological differences, especially in neurocranial shape, are discussed above (p. 70).

Haplochromis paraguiarti also resembles, rather closely, *H. acidens*; the species are compared on p. 76.

Some specimens of *H. prognathus*, a rather variable species, resemble *H. paraguiarti* but there are several differences which serve to distinguish even these superficially similar individuals; *H. paraguiarti* has a shorter head (33·0–36·8, M = 34·8 per cent of standard length, *cf.* 35·5–38·4, M = 36·9 per cent), a shallower preorbital (14·5–19·5, M = 16·9 per cent head, *cf.* 18·8–23·1, M = 20·8 per cent), shorter snout (31·0–36·2, M = 33·5 per cent head, *cf.* 33·4–39·0, M = 37·0 per cent), and a larger eye (23·8–28·6, M = 26·2 per cent head, *cf.* 20·0–25·0, M = 22·6 per cent). Differences in neurocranial form between the species are also distinctive, although the neurocranium of *H. paraguiarti* is intermediate between the more generalized *H. guiarti* type and the relatively elongate skull of *H. prognathus* (see p. 111).

When all characters are considered, *H. paraguiarti*, despite its superficial resemblance to *H. guiarti*, is probably more closely related to *H. prognathus*. It appears to possess the structural characters of the ancestral species or species group from which piscivorous predators like *H. prognathus*, *H. bartoni* and *H. mandibularis* were derived. Outside the piscivorous predator group, it shows very close relationship with *H. acidens* (see p. 76).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.324	Beach near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.6 (Holotype)	Beach near Nasu Point (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.338–344	Beach near Nasu Point	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.313–314	Fisherman's point near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.320–323	Near Grant Bay	E.A.F.R.O.
B.M. (B.H.) 1966.3.9.333–337	Entebbe Harbour	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.317–319	Buka Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.312	Katebo	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.325–330	Beach near Hannington Bay	E.A.F.R.O.
	KENYA	
B.M. (N.H.) 1966.3.9.316	Kamaringa (Kavirondo Gulf)	E.A.F.R.O.
	TANZANIA	
B.M. (N.H.) 1966.3.9.311	Beach N. of Majita	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.315	Majita Beach	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.331–332	Locality unknown	E.A.F.R.O.

Haplochromis acidens sp. nov.

(Text-fig. 13)

Haplochromis percoides (part) : Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 296 (specimens from Kakindu, Victoria Nile, B.M. [N.H.] reg. no. 1911.3.3.82–3).

Paratilapia serranus (part) : Boulenger, 1915, *op. cit.*, *tom. cit.*, 334 (specimens from Ripon Falls, nr. Jinja, B.M. [N.H.] reg. no. 1911.3.3.20–1).

Haplochromis nigrescens (part) : Regan, 1922, *Proc. zool. Soc. Londn.*, 172 (excluding his tentative synonymy of *Astatotilapia roberti* Pellegrin, and the synonymy of *Paratilapia parvidens* Blgr., for which see Greenwood, 1959, p. 194).

NOTES ON SYNONYMY. It is obvious that Regan's (1922) redescription of *H. nigrescens* (Pellegrin), 1909 was influenced by Pellegrin's figure of that species (Pellegrin, 1910, *Mem. soc. Zool. France*, 32, pl. 14, fig. 3). The fish depicted certainly does resemble a specimen of the species here described as *H. acidens*, but the type specimen of Pellegrin's *Astatotilapia nigrescens* more closely resembles *Haplochromis flavipinnis* (personal observations). Boulenger (1915) actually synonymized *A. nigrescens* Pellegrin with *H. percoides* Blgr., 1906 but this action was unacceptable to Regan, who resurrected the species as *Haplochromis nigrescens*. Certainly there are similarities between *A. nigrescens* type specimen and *H. percoides*, but my study of the type was revealed several differences (see appendix for a redescription of this specimen and further comments on its affinities).

In earlier papers I had accepted Regan's resurrection of *H. nigrescens*, and used specimens identified by him as a basis for comparing other Lake Victoria species with *H. nigrescens* ; thus, where *H. nigrescens* is mentioned in those papers, the name should now be corrected to read *H. acidens*.

Two of the three Lake Victoria specimens examined by Regan undoubtedly can be referred to *H. acidens*, but I am uncertain about the identity of the third fish. It is the smallest specimen, and because so little is known about small fishes of this and related groups, diagnostic characters applicable to larger individuals cannot be used with confidence. In many respects, this specimen resembles larger individuals of *H. prognathus*.

HOLOTYPE : an adult male, 108 mm. standard length, from Kisumu Kavirondo Gulf (Kenya), B.M. (N.H.) reg. no. 1966.2.21.1. Named *acidens* from its sharp, needle-like teeth.

DESCRIPTION : based on 17 specimens 67–128 mm. S.L., including the holotype and two of the specimens examined by Regan (B.M. [N.H.] reg. no. 1911.3.3.20–1).

Depth of body 34·6–40·3 (M = 38·1) per cent of standard length, length of head 34·0–36·7 (M = 35·4) per cent. Dorsal head profile gently concave (clearly so in most specimens but weakly concave in a few), sloping fairly steeply ; premaxillary pedicels not prominent.

Preorbital depth 15·2–19·2 (M = 17·1) per cent of head, least interorbital width 21·4–28·2 (M = 24·5) per cent. Snout as long as broad or 1·1–1·2 times longer, its length 31·8–37·2 (M = 34·2) per cent of head, eye diameter 23·0–29·0 (M = 26·4), depth of cheek 23·0–28·2 (M = 25·7) per cent.

Caudal peduncle 14·8–17·9 (M = 16·6) per cent of standard length, 1·1–1·5 (mode 1·3) times as long as deep.

Mouth slightly oblique, lips somewhat thickened, premaxilla with a slight median expansion. Jaws equal anteriorly, the lower 44·0–50·2 (M = 46·9) per cent of head, 1·9–2·4 (rare), mode 2·1, times as long as broad. Posterior tip of the maxilla reaching the vertical through the anterior orbital margin, occasionally not quite reaching this point.

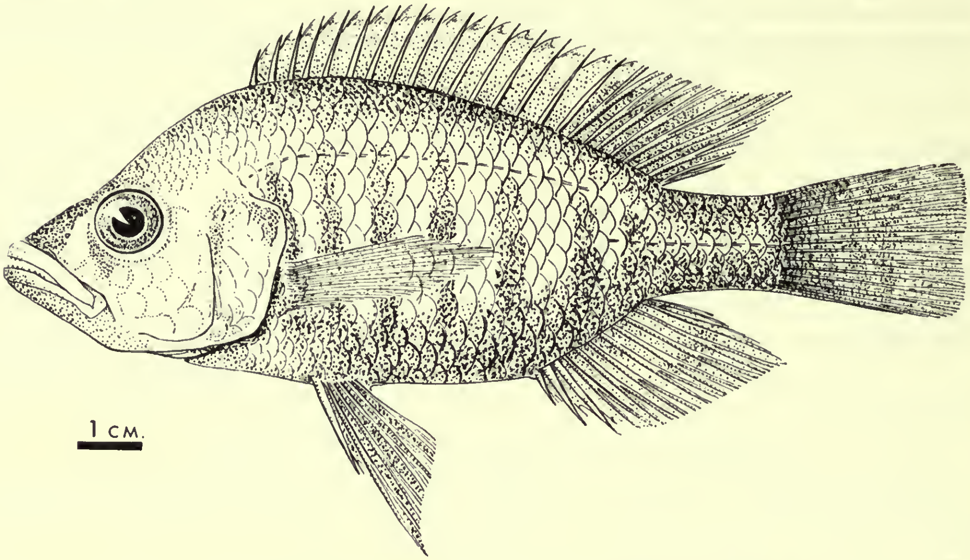

FIG. 13. *Haplochromis acidens.* Drawn by Barbara Williams.

Gill rakers : moderately slender to slender, the lower 1–4 reduced, the upper 3 or 4 flattened and lobed in some fishes ; 10 (rarely 9 or 11) on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 31 (f.1), 32 (f.8), 33 (f.7) or 34 (f.1), cheek with 3 (rarely 4) rows. Five and a half to 7 (mode 6) scales between the dorsal fin origin and the upper lateral line, 5 or 6 (mode), rarely 6½ or 7 between the pectoral and pelvic fin bases.

Fins : Dorsal with 23 (f.1), 24 (f.7) or 25 (f.9) rays, comprising 15 (f.12) or 16 (f.5) spinous and 7 (f.1), 9 (f.11) or 10 (f.5) branched rays. Anal with 11 (f.7) or 12 (f.10) rays comprising 3 spines and 8 or 9 branched elements. Pectoral 22·7–28·0 (M = 24·9) per cent of standard length. Pelvics with the first two branched rays slightly produced, relatively more so in adult males. Caudal truncate to subtruncate, scaled on its proximal half to two-thirds.

Teeth. In the outer row of both jaws the teeth are tall, slender and slightly curved. Fishes between 67 and 90 mm. S.L. have unicuspid teeth anteriorly, and weakly bicuspid teeth laterally and posterolaterally. Larger fishes have only unicuspids in the outer row. The anterior teeth in the upper jaw of the largest specimens may be relatively enlarged (*i.e.* stouter and longer than the lateral teeth). There are 40–64 (M = 48) teeth in the outer, upper row.

The inner rows of the upper jaw are composed of tricuspid teeth in fishes < 90 mm. S.L. and a mixture of uni- and tricuspids in larger fishes; there is an increased proportion of unicuspids in specimens > 115 mm. S.L. In fishes over 100 mm. S.L. the outermost row of the inner series is often composed of unicuspids and the remaining rows of tricuspids. The inner rows are widely spaced in most fishes so that the teeth form a broad band anteriorly and anterolaterally. There are 3 or 4 rows of teeth in the upper jaw.

In the lower jaw of most specimens less than 120 mm. S.L., only tricuspid teeth are found, but some unicuspids also occur in fishes of this size group. Larger individuals have a mixture of tri- and unicuspid or tri- and weakly tricuspid teeth; only rarely are all the lower, inner teeth unicuspid. There are 2 (mode) or 3 rows of inner teeth in this jaw.

Osteology. The neurocranium of *H. acidens* departs from that of *H. guiarti* towards the *H. mento* type (see Greenwood, 1962). The slope of its anterior dorsal profile (from vomer tip to the origin of the supraoccipital crest) is less steep than in *H. guiarti*, and the maximum width (across the otic region) is relatively less, as is its greatest depth (exclusive of the supraoccipital crest). In all these characters, *H. acidens* is intermediate between *H. guiarti* and *H. prognathus*, a species whose neurocranium could provide a basic " bauplan " from which the more extreme " *mento* "-type evolved.

The premaxilla is somewhat beaked, with the dentigerous surface expanded and protracted medially; the pedicels are elongate, being almost as long as the horizontal arms of the bone.

The lower pharyngeal bone is fine, and has the dentigerous surface broader than long. Lower pharyngeal teeth are arranged in 24–28 rows, and are slender, compressed and distinctly cuspidate, with those in the two median rows somewhat coarser than the others.

Vertebral counts from 12 specimens are: 13 + 16 (f.4), 13 + 17 (f.7) and 14 + 16 (f.1), giving totals of 29 and 30.

Coloration. Live colours: Males (sexually active) have a slatey-blue ground colour, darkest dorsally. Dorsal fin smokey-grey with a pale red margin and a deep red flush on the soft part. Caudal dark grey with deep red streaks between the rays. Anal dark hyaline with a dull maroon flush, and orange-red ocelli. Pelvics black.

Females (adult and quiescent): dorsal surface yellowish-grey shading to silver on the flanks and belly. Dorsal fin hyaline but with a yellowish base. Anal and caudal dark hyaline. Pelvics hyaline.

Preserved material: Males (adult and sexually active): ground colour brown (darker than in females and juveniles), darkest dorsally and on chest, belly and ventral half of the caudal peduncle; six to eight vertical bands cross the flanks and caudal peduncle, each band broadening slightly below the level of the upper lateral line, and merging ventrally with the dark body coloration, but remaining discrete dorsally. A narrow, dark lachrymal stripe runs from the anterior border of the eye, sloping backwards to pass behind the posterior tip of the maxilla; a dark narrow stripe outlines the vertical limb of the preoperculum. The spinous dorsal is greyish, the soft part darker on its basal two-thirds, maculate over the posterior half. Caudal maculate on its proximal half to two-thirds. Pelvics dusky, particularly on the basal half; membrane covering the spine colourless. Anal greyish to hyaline, with two, ill-defined and dark grey to dusky ocelli.

Males (*sexually quiescent*) *:* as above but all stripes and bars are much fainter and less well-defined, and the ventral body surface is not noticeably darker than the dorsum, although still darker than the mid-flank region. Only the basal half of each pelvic fin is dusky, and the anal ocelli are almost invisible.

Immature fishes have the same coloration as females.

Ecology. Habitat. The majority of specimens is from a sheltered habitat in the Kavirondo Gulf near Kisumu. At this place the water was about 10 ft. deep, and the substrate of mud; fairly dense stands of submerged plants were common in the area. The other specimens are recorded as being from " Jinja, Ripon Falls ". I am presuming that this locality is in the Napoleon Gulf, that is, above the falls. The area, before the submergence of the Falls, was sheltered, with a hard substrate and, at least close inshore, fairly dense plant stands.

Food. All sixteen specimens examined came from the Kisumu locality, but were caught on different occasions; fifteen specimens contained ingested material in the stomach and intestines. Every gut had, as its major content, finely macerated phanerogam tissue and varying amounts of epiphytic diatoms. Some specimens also contained a flocculent, grey-green mass (as seen in preserved material) thought to be bottom debris, principally blue-green algae. In addition, one gut yielded a few fish bones, one a number of insect eggs (apparently undigested), one a mass of tissue (thought to be the foot of a gastropod) and some fragments of larval Ephemeroptera, and another, fragments of unidentifiable insects.

The phanerogam tissue is very finely divided, and a larger proportion seems to be digested than is the case in other phytophagous species examined.

The apparently vegetarian diet of *H. acidens* is at variance with the dentition and general facies which are essentially those of a piscivorous predator. The length of the gut ($1\frac{1}{2}$ to 2 times standard length) is greater than in the piscivores, but is not as long as the gut in purely phytophagous species.

Breeding. Specimens < 90 mm. S.L. are immature; both sexes reach the same maximum adult size.

Affinities. In its general appearance, *H. acidens* resembles a number of the deeper-bodied piscivorous species, and one of the specialized predators on larval and embryo fishes, *H. parvidens* (Greenwood, 1959).

Perhaps the greatest resemblance is between *H. acidens* and *H. paraguiarti*. Both species have similar neurocrania and jaw structure, but *H. acidens* has finer teeth, a deeper body (34·6–40·3, M = 38·1 per cent of standard length, *cf.* 31·7–36·6, M = 34·8%) and a concave as opposed to a straight dorsal head profile.

Also showing an overall similarity with *H. acidens* is *H. maculipinna*. The concavity of the dorsal head profile in *H. acidens* again serves as one differentiating character. Others are its less oblique jaws, fewer (40–64, M = 48 *cf.* 50–80, M = 62), more slender and longer teeth, and its larger chest scales (5–6 between pectoral and pelvic fin bases, *cf.* 6–9, mode 7 or 8, in *H. maculipinna*). The neurocrania of the two species also differ, that of *H. maculipinna* being deeper and having a steeper dorsal profile ; the premaxilla in this species lacks a pronounced median expansion, and the pedicels meet the horizontal arms almost at right angles (and not at the more acute angle found in *H. acidens*).

From other species of the *H. serranus* group (*H. victorianus*, *H. serranus*, *H. spekii* and *H. nyanzae*), *H. acidens* is distinguished by its concave dorsal head profile, smaller eye, finer, longer and fewer teeth (at least as shown by the mean number, the ranges overlap), less oblique and non-prognathous lower jaw, and by the absence of a prominent mental bump at the symphysis of the dentaries. Other differences also serve to distinguish *H. acidens* from individual species of the *H. serranus* complex ; for these see the species descriptions in Greenwood (1962) and p. 32 above for *H. spekii*.

At about the same level of similarity with *H. acidens* is *H. prognathus*. This species differs from *H. acidens* chiefly in its shallower body (30·1–37·1, M = 33·3% of standard length, *cf.* 34·6–40·3, M = 38·1%), deeper preorbital (18·8–23·1, M = 20·8% of head, *cf.* 15·2–19·2, M = 17·1%) and smaller eye (20·0–25·0, M = 22·6% of head, *cf.* 23·0–29·0, M = 26·4%). The dentition and neurocrania of the species differ quite markedly, with *H. prognathus* having a skull nearer the *H. mento* type (see Greenwood, 1962, and p. 81) and stouter teeth.

It is difficult to assess the phyletic position of *H. acidens*. The level of anatomical specialization, especially of the syncranium and dentition, suggests affinity both with the *H. serranus* species group and with *H. prognathus*, a species not far removed from that group but probably representative of the ancestral type from which such specialized forms as *H. mento* and *H. macrognathus* evolved. Its plant diet suggests a possible trophic specialization paralleling that achieved by a species (*H. phytophagus*) related to the small, anatomically generalized, and usually insectivorous species (Greenwood, 1966).

In an earlier paper (Greenwood, 1959), I suggested that *H. parvidens* might have evolved from a species anatomically like *H. acidens* (called *H. nigrescens* in that paper) ; this relationship is discussed further on page 114.

Phyletically, *H. acidens* was probably derived from the same stem as *H. paraguiarti* ; this stem could have been related to either an *H. guiarti*-like lineage, or to an *H. serranus*-like one.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1911.3.3.20–21	Jinja, Ripon Falls . . .	Bayon
	KENYA	
B.M. (N.H.) 1966.3.9.107–121	Kavirondo Gulf, near Kisumu .	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.1 (Holotype)	Kavirondo Gulf, near Kisumu .	E.A.F.R.O.

Haplochromis prognathus (Pellegrin), 1904

(Text-figs. 14 and 15)

Paratilapia prognatha Pellegrin, 1904 (probably in part; the identity of the three smallest syntypes is still in doubt), *Bull. Soc. Zool. France*, **29**, 185; *Idem*, 1905, *Mem. Soc. Zool. France*, **17**, 181, pl. 16, fig. 4. Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 333, fig. 224 (in part, the syntype B.M. [N.H.] reg. no. 1905.2.28.1, *ex* Kavirondo Gulf).

Pelmatochromis spekii (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 417.

Haplochromis prognathus: Regan, 1922, *Proc. zool. Soc. London*, 177.

Haplochromis taeniatus Regan, 1922, *op. cit.*, 170, text-fig. 3.

Haplochromis macrodon Regan, 1922, *op. cit.*, 176, text-fig. 4.

Haplochromis lamprogenys Fowler, 1936 *Proc. Acad. Nat. Sci. Philad*, ***88***, 330, fig 137.

Haplochromis steindachneri Lohberger, 1929. *Anz. Akad. Wiss. Wein*, no. 17, 207.

Haplochromis versluysi Lohberger, 1929, *Anz. Akad. Wiss. Wein* no. 17, 206.

Haplochromis rebeli Lohberger, 1929, *Anz. Akad. Wiss. Wein.*, no. 11, 94 (probably in part; the identity of one paratype, a female 116 mm. S.L., reg. no. 18768 of the Vienna Museum, is still doubtful).

LECTOTYPE: a fish 136·0 mm. standard length, B.M. (N.H.) reg. no. 1905.2.28.1 (presented by the Paris Museum), collected by C. Alluaud from Kavirondo Bay, Kenya. This specimen appears to be the fish figured by Pellegrin (1905), and is chosen as lectotype principally for that reason.

Note: Defining this species has proved particularly difficult, mainly because of the condsiderable intraspecific variability in head shape (see text-fig. 15). This variability, although apparent to the eye, is not readily quantifiable. Intergrades exist between the most outstanding variants, and now that a large series of specimens is available it appears that the variation is, to a large extent, size correlated. In fishes less than 110 mm. S.L., the snout seems protracted and the dorsal head profile has a marked and extended concavity above the eye. In larger fishes the elongate " face " is less noticeable, and the dorsal profile is straighter and slopes steeply (but still with a slight supraorbital concavity).

DESCRIPTION: based on 43 specimens, 70–141 mm. S.L., and including the lectotype, the syntypes of *H. taeniatus* and *H. macrodon* and the holotypes of *H. steindachneri* and *H. lamprogenys*. The types of *H. rebeli* and *H. versluysi* were examined but are not included in this redescription.

Depth of body 30·1–37·1 (M = 33·3) per cent of standard length, length of head 35·3–38·4 (M = 36·9) per cent; head profile variable (see note above), usually with a supraorbital concavity, the dorsal outline sloping at an angle of 30°–40° with the horizontal.

Preorbital depth 18·8–23·1 (M = 20·8) per cent of head, least interorbital width 18·1–23·7 (M = 21·0) per cent. Snout length 33·4–39·6 (M = 37·0) per cent of head, $1\frac{1}{4}$ to $1\frac{1}{3}$ times as long as broad (rarely $1\frac{3}{8}$ times). Eye diameter with slight negative allometry, 20·0–25·0 (M = 22·6) per cent of head; in fishes 70–90 mm. S.L., the eye is clearly larger than the cheek is deep but in specimens 90–110 mm. it is equal to or slightly smaller than the cheek, a relationship that holds for some larger individuals (110–125 mm. S.L.) although in most individuals in this size range the eye diameter is manifestly less than the cheek depth. Depth of cheek 20·6–28·6 (M = 24·5) per cent of head (18·9% in the smallest specimen).

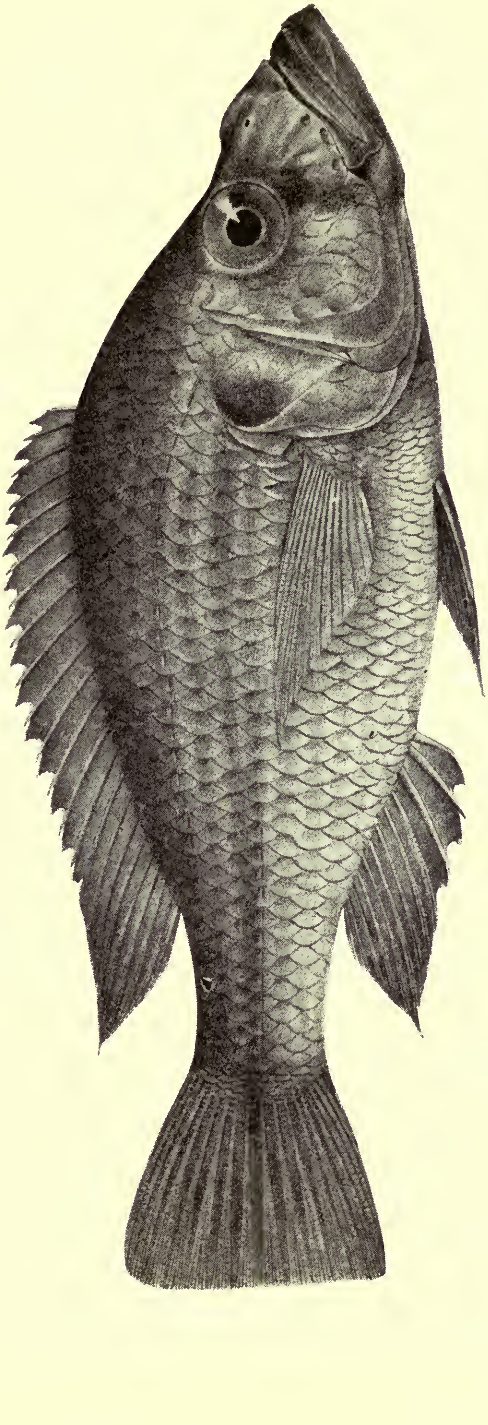

FIG. 14. *Haplochromis prognathus*. Lectotype, about natural size. From Boulenger, *Fishes of the Nile*.

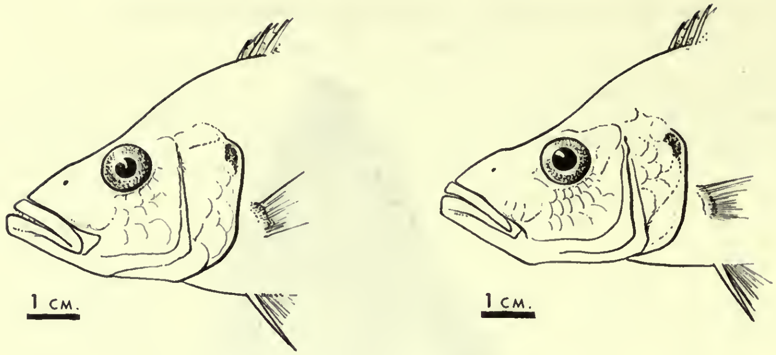

FIG. 15. *Haplochromis prognathus*, showing variability of head profile.

Caudal peduncle 14·6–19·0 (M = 16·0) per cent of standard length, 1·2 (rarely)–1·7 times is long as deep (modal range 1·3–1·5).

Mouth moderately oblique, the jaws equal anteriorly or the lower projecting slightly; lower jaw with a slight mental protuberance, its length 42·5–51·1 (M = 46·2) per cent of head, 2·0–2·8 (mode 2·4) times as long as broad. Posterior tip of the maxilla not reaching the vertical through the anterior orbital margin (except in one specimen), but usually reaching a point nearer this line than one through the nostril.

Gill rakers: 8–10 (mode 9) on the lower part of the first gill arch, the lower 1–3 rakers reduced, the upper 3 or 4 often flat or flat and lobed, the remainder slender.

Scales: ctenoid. Lateral line with 30 (f.2), 31 (f.12), 32 (f.21) or 33 (f.8) scales; some individuals lack pores in the scales of this series. Cheek with 3 (occasionally 4) rows. Five to 7 (mode 6) scales between the dorsal fin origin and the upper lateral line, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.6), 24 (f.26) or 25 (f.10) rays, comprising 14 (f.11), 15 (f.28) or 16 (f.3) spines and 8 (f.1), 9 (f.28) or 10 (f.13) branched rays. Anal with 11 (f.2), 12 (f.21) or 13 (f.11) rays, comprising 3 spines and 8 (f.2), 9 (f.21) or 10 (f.11) branched elements. Pectoral fin shorter than head, 22·0–29·3 (M = 25·7) per cent of standard length. First pelvic branched ray slightly produced in both sexes but proportionately more so in males. Caudal truncate or subtruncate, scaled on its basal half to two-thirds.

Teeth. In the smallest fish examined (70 mm. S.L.) the outer teeth in both jaws are mostly unequally bicuspid, but a few unicuspids are present. Fishes between this size and 105 mm. S.L. have mostly unicuspids in the outer row, but some bicuspids occur posterolaterally in the upper jaw. Fishes > 105 mm. have only unicuspid outer teeth, a condition found occasionally in individuals as small as 90 mm. S.L. The unicuspids are slightly curved inwards, and vary in form from relatively slender to moderately stout. There are 30–60 (M = 45) teeth in the outer row of the upper jaw, the number not showing any correlation with the fish's size. Regan's (1922) "key" character separating *H. taeniatus* from *H. macrodon* (outer teeth numerous, close together *cf.* outer teeth rather strong, set well apart) is hardly trenchant even when only the type specimens are compared, and is inapplicable when a large series is examined.

The inner teeth are mostly tricuspids in fishes < 110 mm. S.L., but an admixture of tri- and unicuspids (or weakly tricuspids) is found in fishes at the upper end of this size range. Some tricuspids also occur in large fishes, but in the majority of these all inner rows are composed of unicuspids. When tri- and unicuspids occur together in fishes > 120 mm. S.L. the tricuspids are confined to the innermost rows. Inner teeth are arranged in 2 (mode) or 3, rarely 1, rows in the upper jaw, and in 1 (mode) or 2 (rarely 3) rows in the lower.

Osteology. The neurocranium of *H. prognathus* is approximately intermediate between that of *H. paraguiarti* and *H. mento* (see p. 70, and Greenwood, 1962). It thus closely resembles the neurocrania of *H. bartoni*, *H. mandibularis*, *H. argenteus* and *H. longirostris* (see p. 112 and Greenwood, *op. cit*), in Lake Victoria, and *H. venator* in Lake Nabugabo (Greenwood, 1965). From the four former species it differs most noticeably in its deeper supraoccipital crest, and from *H. argenteus* also by its being somewhat broader anterior to the orbits. There are also resemblances in neurocranial form between *H. prognathus* and *H. xenostoma* (see p. 53) but the differences here are somewhat more pronounced than in the other species mentioned.

The premaxilla has an expanded median dentigerous surface which gives the bone a beaked appearance ; this is a feature of those piscivorous species which I consider to be more specialized in body-form than the members of the *H. guiarti* and *H. serranus* species complexes (see Greenwood, 1962). In contrast, the dentary of *H. prognathus* is of the stout, deep-bodied type found in the latter groups.

The lower pharyngeal bone is triangular, with the dentigerous surface as long as broad or slightly broader (both conditions are of equal frequency). The lower pharyngeal teeth are fairly coarse, with cylindrical necks and compressed, weakly bicuspid crowns ; these teeth are well-spaced on the bone in 18–24 rows.

Vertebral counts in 8 specimens are : 12 + 17 (f.2), 13 + 15 (f.1), 13 + 16 (f.4) and 13 + 17 (f.1) giving totals of 28–30.

Coloration. Live colours are unknown. *Preserved material : Males* (*adult and sexually active*). Body and head brownish above the midline, silvery-yellow below ; two faint lateral bands are visible, one running midlaterally from behind the eye to the origin of the caudal fin, the other along the upper lateral line. There is a faint, ill-defined but broad lachrymal band, but it does not extend ventrally to the margin of the preorbital. Dorsal fin greyish, the dark pigment most intense basally on the spinous region, lappets dusky ; soft dorsal maculate. Caudal dark grey, darkest between the rays on the proximal two-thirds of the fin. Anal greyish, lappets black, as may be the basal part of the membrane between the spines ; 2 or 3 large but faint, greyish ocelli. Pelvics black.

Females (*adult and juvenile*). Light grey-brown above, silvery below ; very faint traces of longitudinal bands as in males, the lower often visible on the posterior third of the body. All fins hyaline, but the caudal is dark on its proximal two-thirds.

Ecology. Habitat. Haplochromis prognathus is apparently confined to water less than 20 ft. deep, and to hard substrates ; it occurs in both sheltered and exposed localities, including wave-washed beaches.

Food. Of the 33 specimens examined (from 11 localities), 22 contained food. Ten specimens contained only remains of fishes (predominantly small Cyprinidae, but *Haplochromis* were also identified), 3 yielded fish and insect remains (the fish unidentifiable, the insects adult Isoptera and larval Ephemeroptera), 7 contained only insects (adult Isoptera and larval Ephemeroptera), 1 contained unidentifiable fish remains and some plant fragments (undigested), and 2 specimens contained unidentifiable material (? bottom debris) and some plant remains.

Breeding. Little is known about the breeding habits of this species ; no brooding individuals have been recorded. Sexual maturity is attained at a length of about 100 mm., but larger juvenile individuals (up to 120 mm.) are known. Both sexes reach the same maximum adult size.

Affinities. There is nothing particularly outstanding about the general appearance of *H. prognathus* when it is compared with the other relatively deep-bodied predatory species of Lake Victoria. Thus, it bears a superficial resemblance to several piscivorous species, especially *H. serranus*, *H. bartoni*, *H. nyanzae* and *H. mandibularis*.

From *H. serranus*, *H. prognathus* differs in its slightly shallower body (30·1–37·1, M = 33·3% standard length *cf.* 32·7–39·2, M = 36·0%), deeper preorbital (18·8–23·1, M = 20·8% head, *cf.* 14·6–20·0, M = 17·7%), slightly longer snout (33·4–39·0, M = 37·0% head, *cf.* 30·8–37·0, M = 34·0%), shorter lower jaw (42·5–51·1, M = 46·2% head, *cf.* 47·0–60·0, M = 54·3%) and slightly larger chest scales (5–7, mode 6, between the pelvic and pectoral fin bases, *cf.* 7 or 8 [rarely 6]). The preserved coloration of the two species suggests a fairly marked difference in live colours, and there are clear-cut differences in neurocranial form (see p. 110).

From *H. bartoni* (probably its nearest extant relative), *H. prognathus* differs in having a broader and shorter lower jaw (42·5–51·1, M = 46·2% head, *cf.* 50·8–57·0, M = 52·5%), fewer outer teeth in the upper jaw (30–60, M = 45, *cf.* 50–80, M = 62), the maxilla not extending so far posteriorly (reaching or almost reaching the orbit in *H. bartoni*), and its smaller chest scales. Neurocranial form in the two species is similar.

The characters separating *H. prognathus* from *H. nyanzae* are its longer snout (33·4–39·6, M = 37·0% head, *cf.* 33·4–35·8, M = 34·5%), more oblique lower jaw, its maxilla not reaching the orbit, and its larger chest scales. Unfortunately it has not been possible to compare directly the neurocrania of the two species. But, from radiographs it seems probable that the skull of *H. nyanzae* is like that of *H. serranus* (see Greenwood, 1962).

Haplochromis prognathus differs from *H. mandibularis* in having a broader snout, shorter lower jaw (42·5–51·1, M = 46·2% head, *cf.* 47·3–56·8, M = 51·5%), and longer caudal peduncle (14·6–19·0, M = 16·6% standard length, *cf.* 12·2–15·2, M = 14·2%). Neurocranial form in the two species is similar.

Haplochromis prognathus is, apparently, closely related to *H. argenteus*. At first sight, the great variability in head shape of *H. prognathus* obscures the relationship. But, if smaller specimens of *H. prognathus* are compared with larger individuals of *H. argenteus* the likeness is striking. Morphometrically, even superficially dissimilar specimens of the two species are not readily separable. Characteristics of the lower jaw serve to distinguish the species. The lower jaw of *H. prognathus* is broader (length/breadth ratio 2·0–2·8 [modal range 2·0–2·4], *cf.* 2·3–3·1 [modal range 2·8–3·0]), shorter (42·5–51·1, M = 46·2% of head, *cf.* 45·0–59·0, M = 50·2%), less oblique and less prognathous.

The possible phyletic relationship of *H. prognathus* within the Lake Victoria species-flock will be discussed later (p. 110) ; outside Lake Victoria, *H. prognathus* is probably related to *H. venator* of Lake Nabugabo (Greenwood, 1965). Indeed *H. venator* could well have been derived from populations of *H. prognathus* cut off when the sand bar which isolated Lake Nabugabo was formed about 4,000 years ago.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.304 (Syntype *H. macrodon*)	Entebbe	Degen
B.M. (N.H.) 1906.5.30.305–6 (Syntypes *H. macrodon*)	Bugonga	Degen
B.M. (N.H.) 1906.5.30.250 (Syntype *H. taeniatus*)	Entebbe	Degen
B.M. (N.H.) 1966.3.9.50	Entebbe, Airport Beach . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.64–65	Napoleon Gulf, near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.53–59, 66–67, 72–75	Beach near Nasu Point (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.68–71	Katebo	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.79–83	Bugonga, near Entebbe . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.51–52	Kagera Bay, near mouth of Kagera River . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.60–63	Bukafu Bay	E.A.F.R.O.
Vienna Museum 17872 (Type of *H. steindachneri*)	Sesse Islands	Rolle
Academy of Nat. Sciences Philadelphia ANSP 66131 (Holotype of *H. lamprogenys*)	Kitala	——
	KEYNA	
B.M. (N.H.) 1905.2.28.1 (Lectotype)	Kavirondo Gulf . . .	Alluaud
B.M. (N.H.) 1905.12.11.4 (Syntype *H. taeniatus*)	Kavirondo Gulf . . .	Alluaud
	TANZANIA	
B.M. (N.H.) 1966.3.9.76–78	Mwanza Harbour . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.84	Capri Bay, Mwanza . . .	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1906.5.30.251–2, 256	Locality unknown . . .	Degen
Vienna Museum 17876–7 (Types of *H. versluysi*)	Locality unknown . . .	Rolle
Vienna Museum 18830 (Holotype of *H. rebeli*)	Locality unknown . . .	Rolle
Vienna Museum 18769–71 (Paratypes of *H. rebeli*)	Locality unknown . . .	Rolle

Haplochromis argenteus Regan, 1922

(Text-fig. 16)

Paratilapia longirostris (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 332.
Haplochromis argenteus Regan, 1922, *Proc. zool. Soc. Londn.*, 186, fig. 12.

LECTOTYPE: a juvenile female 114·0 mm. standard length, from Bunjako, Uganda (B.M. [N.H.] reg. no. 1906.5.30.266; the specimen figured by Regan).

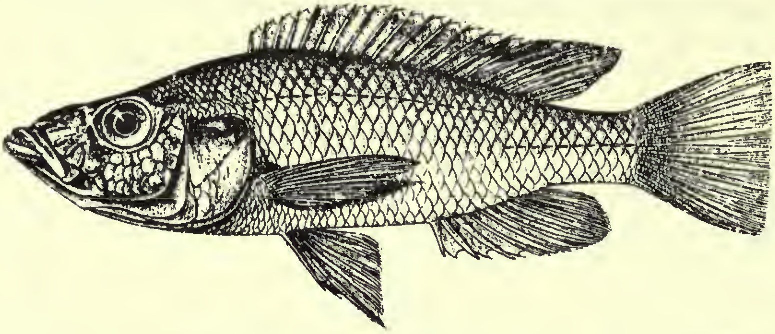

FIG. 16. *Haplochromis argenteus*; the lectotype, a juvenile, about ·75 times natural size. From Regan, *Proc. zool. Soc.*

DESCRIPTION: based on 23 specimens (including the lecto- and paralectotype) 93·0–202·0 mm. standard length.

Depth of body 26·8–34·8 (M = 31·2) per cent of standard length, length of head 35·5–39·6 (M = 36·8) per cent. Dorsal head profile slightly concave, with prominent premaxillary pedicels, and sloping at an angle of 20°–25°.

Preorbital depth 19·6–24·0 (M = 21·7) per cent of head, least interorbital width 17·7–22·3 (M = 20·0) per cent. Snout 1·25–1·40 times as long as broad, its length 34·8–41·6 (M = 37·8) per cent of head, diameter of eye 19·4–23·5 (M = 21·5), depth of cheek 22·3–28·7 (M = 24·7) per cent.

Caudal peduncle 13·5–17·7 (M = 16·1) per cent of standard length, 1·3–1·7 (modal range 1·3–1·5) times as long as deep.

Mouth oblique (35°–40°), the lower jaw projecting moderately in some specimens, its length 45·0–59·0 (M = 50·2) per cent of head, 2·3–3·1 (modal range 2·8–3·0) times as long as broad. Lips slightly thickened. Premaxilla expanded slightly in the midline. Posterior tip of the maxilla reaching a point about midway between the orbit and the nostril, or almost reaching the orbit.

Gill rakers: generally slender but moderately stout in a few fishes; lower 1 or 2 reduced, the upper 3 or 4 (in one fish, the upper 6) flat and lobed. Eight to 10 (mode 9) on the lower part of the first arch.

Scales: ctenoid; lateral line with 29 (f.2), 30 (f.2), 31 (f.5), 32 (f.11), 33 (f.1), 34 (f.1) or 35 (f.1) scales. Cheek with 3 or 4 (rarely 5) rows. Five or 6 (rarely 7) scales between the dorsal fin origin and the upper lateral line, 6 or 7 (less frequently 5) between the pectoral and pelvic fin bases.

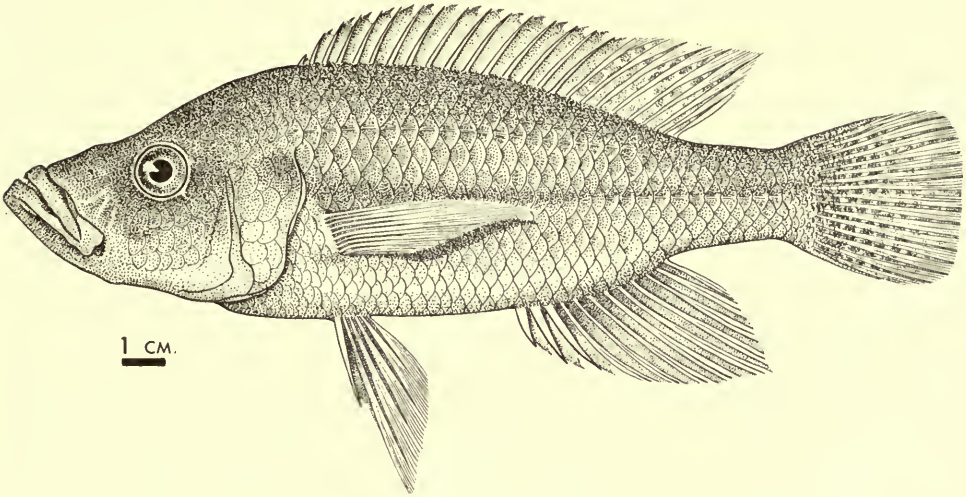

Fig. 16a. *Haplochromis argenteus*, adult. Drawn by Lavinia Beard.

Fins. Dorsal with 23 (f.2), 24 (f.12) or 25 (f.9) rays, comprising 13 (f.1), 14 (f.1), 15 (f.19) or 16 (f.2) spines and 8 (f.2), 9 (f.12) or 10 (f.9) branched rays. Anal with 11 (f.3), 12 (f.19) or 13 (f.1) rays, comprising 3 spines and 8, 9 or 10 rays. Pectoral 24·1–29·7 (M = 25·0) per cent of standard length. Pelvics with the first branched ray somewhat elongate, proportionately more so in adult males. Caudal truncate.

Teeth. Except for the smallest fish examined (the paralectotype 93 mm. S.L.) the outer teeth in both jaws are unicuspid, slender and slightly curved (those situated posterolaterally in the upper jaw more so than the others). In the smallest individual most outer teeth are like those described above but there are also some weakly bicuspid and slender teeth. There are 44–80 (M = 58) teeth in the outer row of the upper jaw, the number showing slight positive correlation with standard length.

In all except four specimens (the two types, 93 and 114 mm. S.L., and two others 88 and 112 mm. S.L.) the inner teeth are unicuspid. Of the exceptional specimens, the largest (lectotype) has an admixture of tri- and unicuspids, the 93 mm. fish (paralectotype) only tricuspids, while the 88 and 112 mm. individuals have tricuspids in the upper jaw and a mixture of tri- and some unicuspids in the lower. Inner teeth are arranged in 2–4 (rarely 5) rows in the upper jaw, and 1–3 in the lower. One exceptional fish (182 mm. S.L.) has a single, irregular row of widely separated teeth in both jaws.

Osteology. The neurocranium of *H. argenteus* is virtually identical with that of *H. longirostris* (see Greenwood, 1962), and also resembles the skull of *H. prognathus*.

The premaxilla is more beaked than that of *H. longirostris*.

The lower pharyngeal bone is narrow, but its dentigerous surface is generally broader than long; less frequently it is equilateral. The teeth are rather coarse, although they are finer and more compressed in a few fishes. These teeth are arranged in 20–24 (usually 22) rows.

Vertebral counts in 8 specimens are: 12 + 17 (f.3) and 13 + 16 (f.5) giving a total of 29.

Coloration. Live colours are unknown. *Preserved material: Males* (*adult and sexually active*): ground colour grey-silver, darker (almost brown) on back and dorsal head surfaces; tip of lower jaw and anterior part of each ramus dusky. Branchiostegal membrane sooty in the opercular region, dark (but not black) anteriorly. Sub- and interopercula with a golden-yellow flush. An ill-defined to distinct lachrymal stripe runs from the anterior orbital margin to behind the posterior tip of the maxilla. Dorsal fin greyish-yellow, with black lappets, and in some specimens a dusky, irregular banding or marbling on the entire spinous and anterior soft parts. Caudal greyish-yellow, dark grey-brown on the proximal half. Anal greyish with black lappets, and 2 or 3 dead-white ocelli. Pelvics dusky.

Males (*sexually quiescent, and immature*): Ground colours like those of active individuals but somewhat lighter, often with very faint traces of 4 or 5 bars midlaterally on the flanks; the lachrymal stripe is of variable intensity. Dorsal fin as above or without the dark marbling. Other fins also as above, but the anal ocelli may be weakly defined and small, and the pelvics lighter.

Females (*adult and immature*). Ground coloration as in males, but with a faint, interrupted and narrow midlateral band running from the posterior opercular margin to the basal part of the caudal fin. Even fainter traces of a more dorsal longitudinal band (following the course of the upper lateral line) are seen in some specimens; the two bands may be linked by 3 or 4 extremely faint, short and narrow vertical bars. All fins are yellowish, the caudal dark basally.

Ecology. Habitat. Most specimens are from sheltered localities where the bottom is composed of organic mud, and at depths of less than 40 ft. Other localities are, however, more exposed and the substrate is of rock, sand or shingle, but only a few (and juvenile) fishes were obtained from nets operated over exposed beaches.

Food. Of the 20 individuals examined (from 11 localities) 8 had food in the gut. Four fishes contained only insect remains (in 2 thought to be terrestrial species, and in the others identified as larval Ephemeroptera), and 4 had fragmentary fish remains (identified as the cyprinid *Engraulicypris argenteus*).

Breeding. Fishes < 114 mm. S.L. are immature, as is one exceptional specimen of 146 mm. Both sexes reach the same maximum adult size.

Affinities. The species most like *H. argenteus* is *H. longirostris.* There are, however, a number of morphological differences which serve to separate them, including the larger adult size reached by *H. argenteus.* From *H. longirostris*, *H. argenteus* also differs in its less oblique and longer lower jaw (45·0–59·0, M = 50·2% of head, *cf.* 42·2–51·4, M = 46·0%), shorter and deeper caudal peduncle (13·5–17·7, M = 16·1% of standard length, *cf.* 17·2–22·2, M = 19·2%; length/depth ratio 1·3–1·7 [modal range 1·3–1·5], *cf.* 1·7–2·3 [modal range 1·9–2·0]), somewhat deeper body (26·8–34·8, M = 31·2% of standard length, *cf.* 24·6–30·4, M = 27·2%) and slightly longer head (35·5–39·6, M = 36·8% standard length, *cf.* 29·2–36·2, M = 33·0%); also, the premaxilla of *H. argenteus* is somewhat more beaked. In an earlier paper (Greenwood, 1962) I used the ratio of eye diameter to interorbital width as a diagnostic character ; more material of *H. argenteus* has shown, however, that this difference is too slight to be of value.

The similarities between *H. argenteus* and *H. prognathus* are discussed elsewhere (p. 82). When these two species and *H. longirostris* are considered together, it seems probable that *H. argenteus* and *H. longirostris* were derived from an *H. prognathus*-like ancestor, probably as distinct lines developing almost in parallel.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.266 (Lectotype)	Bunjako	Degen
B.M. (N.H.) 1906.5.30.267 (Paralectotype)	Bunjako	Degen
B.M. (N.H.) 1966.3.9.194–195	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.201–202	Pilkington Bay . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.193	Beach near Nasu Point . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.196–198	Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.192	Off S. end of Buvuma Island .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.208–210	Beach near Grant Bay (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.191	Channel between Yempita and Busiri Islands . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.199–200	Kazima Island . . .	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.203–204	Off Entebbe Harbour . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.207	Entebbe Harbour . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.205–206	Bukakata Bay	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1901.6.24.90	Locality unknown . . .	Sir. H. Johnston
B.M. (N.H.) 1966.3.9.190	Locality unknown . . .	E.A.F.R.O.

Haplochromis squamulatus Regan, 1922

(Text-fig. 17)

Paratilapia pectoralis (non *Ctenochromis pectoralis* Pfeffer) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 66, pl. 1, fig. 2. *Idem*, 1915, *Cat. Afr. Fish*, **3**, 339, fig. 229.

Paratilapia serranus (part) : Boulenger, 1915, op.cit., tom. cit., 334.

Haplochromis guiarti (part): Regan, 1922, *Proc. zool. Soc. Londn.*, 174.

Haplochromis squamulatus Regan, 1922, *op. cit.*, 175 (*nom. nov.* for *Paratilapia pectoralis* Blgr., 1911).

HOLOTYPE : a male (probably adult), 149 mm. standard length, from Jinja (Uganda). Genoa Museum reg. no. C.E. 12977.

DESCRIPTION : based on 54 specimens (including the holotype), 66–198 mm. S.L.

Depth of body 23·5–35·1 (M = 30·3) per cent of standard length, length of head 29·4–39·5 (M = 34·3) per cent. Dorsal head profile moderately to strongly sloping, the premaxillary pedicels prominent and breaking the outline of the profile, snout region sloping at an angle of 40°–50° with the horizontal.

Preorbital depth in fishes < 100 mm. S.L. ($N = 11$), 12·5–16·5 ($M = 15·5$) per cent of head, in larger fishes ($N = 43$) 15·6–21·6 ($M = 18·9$) per cent, least interorbital width 21·2–28·3 ($M = 25·0$) per cent. Snout as long as broad to 1·3 times longer, its length in fishes < 100 mm. S.L., 26·0–32·1 ($M = 29·1$) per cent of head, in larger individuals 20·6–25·9, $M = 23·3$ per cent. Cheek depth 19·5–29·3 ($M = 25·7$) per cent of head.

Caudal peduncle 14·3–22·3 ($M = 17·9$) per cent of standard length, 1·2 (rare)–2·0 (mode 1·7) times as long as deep.

Mouth horizontal or very slightly oblique, jaws equal anteriorly, or infrequently, lower projecting slightly. Length of lower jaw in fishes < 170 mm. S.L. ($N = 46$), 39·0–48·0 ($M = 44·1$) per cent of head, 44·2–51·0 ($M = 47·5$) per cent in larger fishes ($N = 8$) ; 1·5–2·5 (mode 1·8, modal range 1·5–2·0) times as long as broad in fishes of all sizes. Posterior tip of the maxilla generally reaching the vertical through the anterior orbital margin or to below the eye, but not reaching either point in a few individuals. Lips slightly thickened ; premaxilla not expanded medially.

Gill rakers : short and stout, often flat, in most specimens ; in fishes < 120 mm. S.L., but also in a few larger individuals, most of the rakers are relatively slender. Eight–10 (mode 9), rarely 11, on the lower part of the first arch, the lower 1–3 rakers reduced.

Scales : ctenoid. Lateral line with 32 (f.2), 33 (f.12), 34 (f.8), 35 (f.15), 36 (f.10), 37 (f.6) or 38 (f.1). Pore distribution in this series is irregular, with some pore scales occurring in the horizontal row above that in which the majority lies ; also, some scales are without pores and are often smaller than those before and behind them. Cheek with 3 (f.8), 4 (f.32), 5 (f.12) or 6 (f.1) rows of scales. Scales on the nape, chest and belly are small ; 6 (f.3) 6½ (f.3), 7 (f.11), 7½ (f.5), 8 (f.14) or 9 (f.16) between the

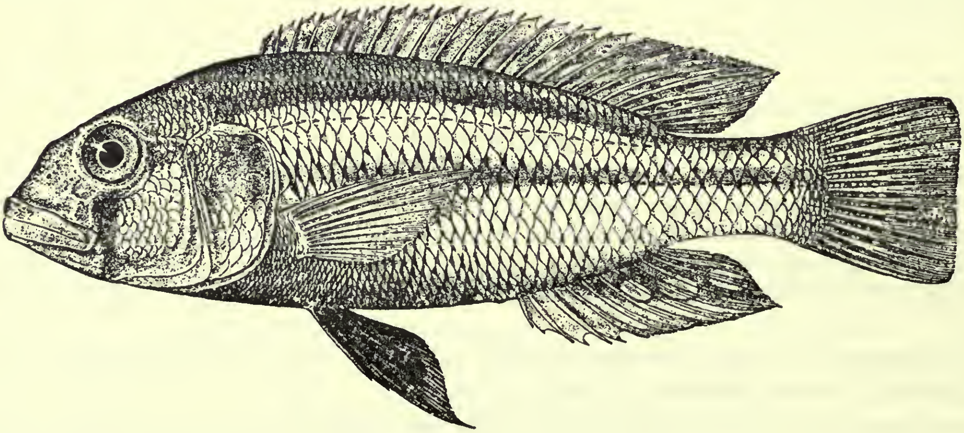

FIG. 17. *Haplochromis squamulatus*, holotype, about ·72 times natural size. From Boulenger, *Cat. Afr. Fish.*

dorsal fin origin and the upper lateral line, 6 (f.1), 7 (f.8), 8 (f.16), 9 (f.25) or 10 (f.3) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.9), 25 (f.37) or 26 (f.6) rays, comprising 14 (f.2), 15 (f.26) or 16 (f.24) spines, and 8 (f.2), 9 (f.23), 10 (f.25) or 11 (f.2) branched rays. Anal with 11 (f.3), 12 (f.40) or 13 (f.5) rays, comprising 3 spines (except for one specimen with 2), and 8 (f.3), 9 (f.40) or 10 (f.5) branched elements. Pectoral 21·8–27·0 (M = 24·7) per cent of standard length. Pelvics with the first branched ray produced in both sexes but proportionately more so in adult males. Caudal subtruncate to truncate.

Teeth. Most fishes < 105 mm. S.L. have either an admixture of uni- and bicuspid teeth in the outer row of both jaws, or only bicuspids. One specimen (89 mm. S.L.) has predominantly bicuspids and a few tricuspids in the upper jaw, but mostly unicuspids in the lower. In larger fishes of the < 105 mm. group, unicuspid teeth predominate in both jaws, and in fishes > 105 mm. S.L. only unicuspids are found. All outer teeth are relatively slender and gently curved, the unicuspids more so than the bicuspids. The mean number of teeth in the outer row of the upper jaw shows some positive correlation with standard length although there is little difference in the ranges for the various groups ; fishes < 120 mm. S.L. have 50–72, M = 57 teeth in this row, while larger specimens have 52–80, M = 68.

There is less obvious correlation between tooth form and the fish's size when the inner rows of teeth are considered. All fishes < 105 mm. S.L. have only tricuspids in the inner rows. Above this length many fishes have only unicuspids, but a mixture of uni- and tricuspids (or weakly tricuspids) is common even in the largest individuals. Unicuspids occur most frequently in the outer rows of the inner series.

Inner teeth are arranged in 2–6 rows (usually 3 or 4) in the upper jaw, and in 1–6 (usually 2 or 3) in the lower jaw. There is perhaps some correlation between the number of rows and the fish's length because the largest specimens (179–198 mm. S.L.) have the greatest number of inner rows. Also, in larger fishes the inner teeth are implanted very obliquely but are almost vertical in fishes < 105 mm. S.L.

Osteology. The neurocranium of *H. squamulatus* combines characteristics of both the *H. guiarti* and the *H. serranus* types (see Greenwood, 1962). The dorsal preorbital profile rises steeply and is gently curved ; its line is continuous with that of the supraoccipital crest whose anterior point lies further forward than in the skulls of *H. guiarti* and *H. serranus*. In general there is a great similarity between the neurocrania of *H. squamulatus*, *H. michaeli* and *H. martini* (see Greenwood, *op. cit*).

The premaxilla is of the generalized type, and thus lacks a pronounced anterior extension of its medial dentigerous surface.

The lower pharyngeal bone has the dentigerous surface broader than long, from slightly to markedly so. The lower pharyngeal teeth are relatively slender, compressed and distinctly cuspidate ; the teeth are arranged in 22–26 (mode 24) rows.

Vertebral counts in 10 specimens are : 13 + 16 (f.2), 13 + 17 (f.2), 13 + 18 (f.2), 14 + 16 (f.1), 14 + 17 (f.3) giving totals of 29–31.

Coloration. Live colours are known for females (adult) and quiescent males. *Females :* ground colour yellow-silver above shading to yellowish-white ventrally, the dorsal body and head surfaces are darkest. Two distinct longitudinal bands are invariably present, the lower running from the operculum to the caudal fin origin along the level of the lower lateral line, the upper extending from the nape to the end of the dorsal fin at a level about two scale rows below the dorsal fin insertion. Both bands have a finely zig-zagged outline ; the upper band may be faint. Dorsal fin dark neutral. Caudal dark neutral with a yellow flush. Pelvic and anal fins yellow.

Quiescent males have a coloration like that of the females described above.

Preserved material : Males (*adult, sexually active but not ripe*). The general impression is one of dusky greyness, with small areas of light brown on the flanks. The entire head is dark but is lighter on the operculum and lower lip (the lower jaw is dark). A broad black band (faint in some specimens) runs from the posterior opercular margin to the caudal fin origin ; it is crossed by 3 or 4 broad but faint vertical bars in the zone of lighter flank coloration. These bars merge with the dark dorsum and sooty-grey chest and belly. The ventral aspects of the caudal peduncle are also sooty-grey. Dorsal fin yellow-brown with a sooty overlay, the lappets are black, and a few ill-defined dark maculae may be visible on the posterior part of the soft dorsal fin. Caudal dark grey-brown on its proximal three-quarters, yellowish-brown distally. Anal coloured like the dorsal but greyer over the spinous part ; ocelli either not clearly defined, or white with a sooty surround. Pelvic fins dusky over a yellowish ground.

Males (*adult but quiescent*). Ground colour light brown, shading to golden on the ventral surfaces which are, however, overlaid with greyish-black. Dorsal surface of the head and body dark brown. A fairly broad, distinct and almost vertical lachrymal stripe runs from the anteroventral orbital margin to the dentary. A very distinct, broad lateral stripe runs from the opercular margin to the caudal fin base ; the upper margin of this band is irregularly serrate. There are 3 or 4 incomplete but broad and distinct vertical blotches on the ventral half of the flanks, each blotch originating from the midlateral band but not extending to a point more than half way between the lateral band and the ventral body outline. A very faint dark upper lateral band may be distinguished running at a level about midway between the dorsal fin base and the upper lateral line ; this band is often indistinguishable from the generally dark coloration of the dorsum. A third band at the base of the dorsal fin may be visible. Dorsal fin pale brownish-yellow, with a faint sooty overlay ; lappets black, dark blotches present on the soft fin. Anal pale yellowish, with a very faint sooty overlay. Pelvics yellowish with an intense sooty overlay on the anterior half. Caudal dark greyish-yellow.

Immature males are coloured like females (see below),but have a darker ground coloration (almost grey on the chest and belly) and faintly sooty pelvics.

Females (*adult and immature*). Female coloration is very distinctive because of the well-marked lateral bands. The ground coloration is a yellowish-silver, somewhat greyish above the upper lateral line and on the dorsal head surface ; the cheek and operculum are yellow-silver. The midlateral band is black and has characteristically serrate upper and lower margins ; the depth of this band is rather variable in any one fish, and is generally deepest above the anal fin. The upper lateral band also has irregularly serrate margins but it is generally less obvious because of its position on the dark colour of the dorsum. A third longitudinal band, narrower and interrupted, lies along the base of the dorsal fin as a series of narrow, elongate blotches. Dorsal fin yellowish with a faint sooty overlay, and sooty lappets; the soft part often has dark spots and blotches between the rays. Caudal yellowish with dark maculae on the proximal quarter to third. Anal and pelvic fins yellow.

Ecology. Habitat. The species is known from a wide variety of habitats, including sheltered bays and gulfs, exposed beaches, and from certain off-shore localities near small islands. In most places the substrate is hard (rock, sand or shingle) but *H. squamulatus* is known to occur over mud bottoms.

Food. Thirty-six specimens were examined (covering the entire size-range, and from 18 localities); of these, 19 contained food in the gut. In 16 fishes the food consisted entirely of fishes, the remains so macerated that certain identification was difficult; in two cases the remains were identified as *Haplochromis* species, in one as *Engraulicypris*, and in another as a cichlid. In two female fishes the stomach contained many small embryos of cichlid fishes; these could well be the fishes' own broods swallowed at the time of capture, although it is not known whether *H. squamulatus* is a mouth-brooder. A third female fish had several small post-larval cichlids in the stomach; judging from the gonad state of the predator it seems unlikely that the larvae were its own brood.

In addition to the sixteen piscivorous fishes, one other yielded only crustacean remains, one several insect egg-masses, and a third the remains of boring mayfly larvae (*Povilla adusta*).

Breeding. All specimens, except one, below 135 mm. S.L. are immature; the exceptional fish (93 mm.) is a ripening female. The largest fishes (180–198 mm. S.L.) are females but there is one male of 179 mm. S.L.

Affinities. The colour pattern, small chest and nuchal scales and the sharply decurved head profile of *H. squamulatus* make at least large specimens readily identifiable. But, smaller individuals are less easily distinguished from specimens of *H. martini* (although the latter are adult at a size when most *H. squamulatus* are still immature). Unfortunately, little is known about the live coloration of sexually active male *H. squamulatus* but there are several similarities in the coloration of female *H. martini* and *H. squamulatus*, particularly in the striping and the yellowish coloration. In fishes of all sizes, *H. squamulatus* differ from *H. martini* in their less strongly decurved head profile, maxilla not extending so far posteriorly (never reaching a point below the pupil as is general in *H. martini*), in having a higher modal number of lateral line scales (35 *cf.* 33) and of scales between the pectoral and pelvic fin bases (9 *cf.* 7 or 8), and in the somewhat shallower body (23·5–35·1, M = 30·3% standard length, *cf.* 30·8–38·0, M = 34·4%).

When specimens over 100 mm. S.L. are compared, a number of additional morphometric differences are apparent: *H. squamulatus* has a longer snout, smaller eye and a longer lower jaw. Specimens less than 100 mm. S.L. have only one trenchant morphometric difference, the size of the eye (eye diameter in *H. squamulatus* is 25·9–30·4 [M = 28·3]% of head, *cf.* 29·4–37·5 [M = 31·7]% in *H. martini*).

Also resembling *H. squamulatus* (and *H. martini*, see Greenwood, 1962) is *Haplochromis michaeli*. The species differ in their preserved coloration (see above, and

Greenwood, *op. cit.*, p. 205), in the straighter, slightly concave, dorsal head profile of *H. michaeli*, and the greater posterior extension of the maxilla in that species (generally to below the pupil). Since specimens of *H. michaeli* over 100 mm. S.L. only are known, interspecific morphometric comparisons are restricted. These, however, show that *H. squamulatus* has a slightly shallower body (23·5–35·1, M = 30·3% of standard length, *cf.* 30·8–37·6, M = 34·3%), and a smaller eye (20·6–25·9, M = 23·3% head, *cf.* 24·0–29·1, M = 27·0% in *H. michaeli*). The nuchal scales of *H. squamulatus* are somewhat smaller (modal number of scales between the dorsal fin origin and the upper lateral line 8 or 9, *cf.* 6 or 7 in *H. michaeli*) as are those of the lateral line series (mode 35 *cf.* 33) ; the upper limit of the range for the lateral line scale count is also higher in *H. squamulatus* (38 *cf.* 35).

All in all, the resemblances between *H. squamulatus* and *H. martini* are greater than than those between *H. squamulatus* and H. *michaeli*, but the three species seem to form a closely related group within the more generalized piscivorous predators of Lake Victoria.

There is a certain similarity, albeit superficial, between *H. squamulatus* and *H. altigenis*. On closer examination, however, it does not seem likely that the resemblance can be construed as implying a close phyletic connection between the species. *Haplochromis altigenis* is probably a derivative of the *H. guiarti* stem.

In its general facies, *H. squamulatus* shows some similarity with *H. dichrourus*, but there is a very pronounced interspecific difference in coloration (*cf.* p. 90 with p. 67), as well as differences in some morphometric characters. *Haplochromis squamulatus* has a larger eye (20·6–25·9, M = 23·3% of head, *cf.* 19·4–22·6, M = 21·1) a shorter lower jaw (44·2–51·0, M = 47·5% of head, *cf.* 51·3–54·0, M = 52·7%) and a higher modal number of lateral line scales (35 *cf.* 33).

Phyletically, *H. squamulatus* and *H. michaeli* may represent slightly divergent developments (less so morphologically and ecologically in the former species) from an *H. martini*-like stem, an increase in adult size being a common factor in the two lines.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.262–272	Napoleon Gulf near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.282–284	Fisherman's Point near Jinja .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.285–288	Beach near Nasu Point (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.289–295	Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.259–260	Off Buvuma Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.261	Grant Bay	E.A.F.R.O.
Genoa Museum C.E. 12977 (Holotype)	Jinja (Napoleon Gulf) . . .	Bayon
B.M. (N.H.) 1906.5.30.233–9	Nsonga	Degen
B.M. (N.H.) 1909.5.4.4–5	Sesse Islands	Bayon
B.M. (N.H.) 1966.3.9.278–281	Beach in Entebbe Harbour .	E.A.F.R.O.

B.M. (N.H.) 1966.3.9.258	Entebbe, Airport Beach . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.273–277	Kazima Island near Entebbe .	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.255	Old Bukakata Bay . . .	E.A.F.R.O.
	TANZANIA	
B.M. (N.H.) 1966.3.9.257	Capri Bay, Mwanza . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.256	Mwanza Harbour . . .	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1901.6.24.86	Locality unknown . . .	Sir H. Johnston

Haplochromis barbarae sp. nov.

(Text-figs. 18 and 19)

HOLOTYPE: an adult female, 97 mm. standard length, from a beach near Nasu Point (Buvuma Channel); B.M. (N.H.) reg. no. 1966.2.21.5.

Named in honour of Mrs. Barbara Williams, whose drawings illustrate this and others of my papers.

DESCRIPTION: based on 9 specimens (including the holotype) 89·0–106·0 mm. standard length.

Depth of body 32·1–35·5 (M = 34·0) per cent of standard length, length of head 31·4–35·0 (M = 33·5) per cent. Dorsal head profile very slightly decurved or straight.

Preorbital depth 15·1–18·0 (M = 16·9) per cent of head length, least interorbital width 24·2–26·7 (M = 25·5) per cent. Snout as long as broad, its length 30·0–32·4 (M = 31·5) per cent of head, eye diameter 22·9–27·4 (M = 25·8), cheek depth 20·0–25·0 (M = 22·2) per cent.

Caudal peduncle 15·7–18·0 (M = 16·8) per cent of standard length, 1·4–1·7 times as long as deep (no well-defined mode).

Mouth very slightly oblique, the jaws equal anteriorly; lower jaw 36·6–41·2 (M = 38·0) per cent of head, 1·5–1·7 (in one fish 2·0) times as long as broad. Posterior tip of the maxilla reaching a point near the vertical through the anterior orbital margin.

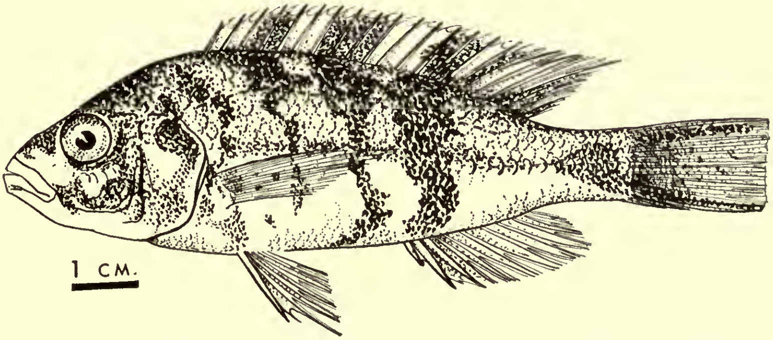

FIG. 18. *Haplochromis barbarae*. Drawn by Barbara Williams.

Gill rakers : of variable form, from moderately short and stout to slender and relatively elongate, but of constant form (except for the reduced lower rakers) in any one individual ; 8 or 9 rakers on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 33 (f.3), 34 (f.2) or 35 (f.4), cheek with 3 or 4 (rarely 2) rows. Seven (rarely 6½ or 8) scales between the upper lateral line and the dorsal fin origin, 7 or 8 (rarely 6 or 9) between the pectoral and pelvic fin bases. Scales on the ventral aspects of the chest are noticeably smaller than those situated laterally.

Fins. Dorsal with 25 (f.7) or 26 (f.2) rays, comprising 16 spinous and 9 (f.7) or 10 (f.2) branched rays. Anal with 11 (f.2), 12 (f.6) or 13 (f.1) rays, comprising 3 spines and 8 (f.2), 9 (f.6) or 10 (f.1) branched elements. Pectoral 25·0–29·2 (M = 26·7) per cent of standard length. Caudal truncate, scaled on its proximal half.

Teeth. In the outer row of both jaws, the teeth are relatively stout, bicuspid and slightly curved ; in a few specimens some posterolateral upper teeth are unicuspid and enlarged. There are 40–65 (M = 50) teeth in the outer row of the upper jaw.

Teeth forming the inner rows are relatively large and tricuspid, and are implanted somewhat obliquely so that the crowns point inwards. There are 2 or 3 inner rows in the upper jaw, and 2 (3 in one specimen) in the lower.

Osteology. No complete skeleton is available. The lower pharyngeal bone is, compared with that of similar species, small. Its dentigerous surface is broader than long, and narrows rapidly at about the midpoint so that not only is the whole bone relatively small, but so is the area of pharyngeal teeth. The teeth are fine, compressed and distinctly cuspidate ; they are rather sparsely distributed in from 22–24 rows.

Vertebral counts in 9 specimens are : 13 + 17 (f.8) and 13 + 18 (f.1) giving totals of 30 and 31.

Coloration : Live colours are unknown. *Preserved colours : Males* (*adult but quiescent*). Ground colour dark yellowish-brown. A well-defined lachrymal stripe is present, as are faint traces of two transverse, parallel stripes across the snout. There is some darkening over the preoperculum but this is not concentrated into a

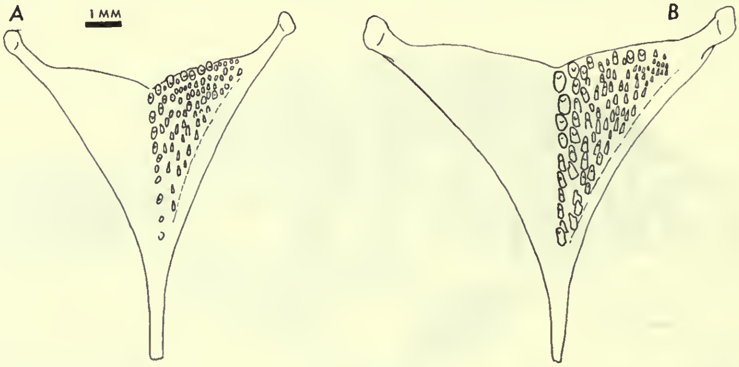

Fig. 19. Lower pharyngeal bones (in occlusal view, with dentition shown on one side only) of (A) *H. barbarae,* and (B) *H. chromogynos.*

bar or stripe. The branchiostegal membrane is dark, most intensely so below the opercular bones. On the flank is a faint midlateral stripe, and four even fainter and incomplete vertical bars. Dorsal and anal fins are yellowish with a sooty overlay, the anal being darkest along its proximal third ; anal ocelli very faint. Pelvics sooty over a yellowish ground. Caudal yellowish on the margins and distal third, dark brown proximally.

Females (*adult.*) Three distinct colour patterns occur ; two of these are probably identical with the polychrome patterns described for live *Hoplotilapia retrodens* (see Greenwood, 1956).

The colour pattern corresponding with the modal coloration in other polychromatic species has a yellow-brown ground colour with a distinct midlateral dark stripe running from the opercular margin to the caudal origin, and extending onto the caudal fin itself for about half its length ; in two specimens there are four, narrow vertical bars on the flanks, extending from the dorsal fin base almost to the ventral outline. In all specimens a very faint upper line is situated slightly above the upper lateral line. All fins are yellowish-brown. Three out of the eight female specimens have this type of coloration.

The second pattern is a piebald, black on silvery-yellow (to yellow brown), the black pigment arranged in blotch-like bars of variable width and dorso-ventral extent. Some blotches extend onto the dorsal, caudal, anal and pelvic fins. The cheeks and snout may be blotched or clear. All fins are yellowish. This pattern does not differ from that shown by other species with a piebald coloration in females. Four of the eight *H. barbarae* females are piebald.

The third pattern, found only in one specimen, has an orange-yellow background peppered with fine melanophores which are, in places, aggregated into blotches (especially on the dorsum) with an irregular distribution. Some dark blotches occur on all fins (but especially the dorsal and caudal) ; these spots are smaller than those on the body. The ground colour of all fins is light orange-yellow.

Ecology. Habitat. The nine known specimens came from three different sites. Two of these are shallow, exposed and sandy beaches, the third, shallow water (*ca.* 10 ft. deep) over a hard substrate a short distance off-shore and near the water-lily zone fringing a papyrus swamp.

Food. Seven of the 9 specimens examined contained ingested matter in the guts. In each case this consisted of from 1–8 (mode 5) recently fertilized cichlid ova. In two specimens these could have been part of the fish's own brood swallowed during capture, because the fishes have recently spent ovaries. But, judging from the advanced stages of oogenesis shown by four other specimens, and the fact that the fifth is a male, it seems reasonable to conclude that the embryos were taken as food (see Greenwood, 1959, for a discussion of other paedophagous *Haplochromis* species).

Breeding. Nothing is known about the breeding habits of *H. barbarae.* All nine specimens are sexually mature ; the sole male (102 mm. S.L.) is the second largest specimen.

Affinities. Anatomically, *H. barbarae* is very like *H. brownae,* a generalized species exhibiting many characters suggestive of affinity with anatomically generalized predators such as *H. guiarti* (Greenwood, 1962).

Haplochromis barbarae differs from *H. brownae* in having a narrower interorbital (24·2–26·7, M = 25·5% of head, *cf.* 26·0–34·0, M = 29·8%), a smaller eye (22·9–27·4, M = 25·8% of head, *cf.* 26·0–31·3, M = 28·6%), fewer gill rakers (8 or 9, *cf.* 9–12 [modes 10 and 11]), and smaller scales, especially on the ventral aspects of the chest. There is also a difference in dention in that the outer teeth of this species are stout bicuspids whereas in *H. brownae* of a similar size the teeth are slender unicuspids.

It differs from *H. guiarti* in having a shorter snout (30·0–32·4, M = 31·5% of head, *cf.* 31·7–37·5, M = 34·4) and lower jaw (36·6–41·2, M = 38·0% of head, *cf.* 39·2–48·2, M = 44·4%), fewer gill rakers (8 or 9, *cf.* 9–11, mode 10) and, at comparable sizes, the presence of bicuspid teeth anteriorly in both jaws (unicuspid in *H. guiarti*).

Because of its generalized anatomy and unspecialized dentition, *H. barbarae* closely resembles a number of other species in the Lake Victoria flock, *viz. H. cinereus, H. macrops, H. lacrimosus* and *H. chromogynos* (see Greenwood, 1959 for the latter species and Greenwood, 1960 for the three former). In addition to their anatomical similarities, *H. barbarae* and *H. chromogynos* also share (with several other and structurally unrelated species) the piebald coloration in females. However, *H. barbarae* differs from *H. chromogynos* in having a longer lower jaw (36·6–41·2, M = 38·0% of head, *cf.* 30·0–34·4, M = 32·5%), and, when specimens of equal size are compared, bicuspid instead of slender unicuspid teeth (specimens of *H. chromogynos* < 95 mm. S.L. have a mixed bi- and unicuspid dentition but larger individuals have only unicuspid teeth). The shape of the pharyngeal bone differs in the two species, and it is this character (see p. 94 and fig. 19) which most readily distinguishes *H. barbarae* from the other three species mentioned above, none of which is known to have piebald females or paedophagous habits.

The peculiar feeding habits of *H. barbarae* immediately suggest some affinity with the other paedophagous *Haplochromis* species, and because *H. barbarae* is anatomically unspecialized, particularly with the more " generalized " paedophages, *H. obesus* and *H. cronus*. However, in many morphological details these two differ considerably from *H. barbarae.* For instance, the peculiar dental morphology of *H. obesus* (with the small teeth deeply embedded in the gums), and the stout unicuspid teeth of *H. cronus,* serve as immediately diagnostic characters, as do the several morphometric differences between the species. It is of interest, however, to recall that piebald females occur in all three species ; but, since this character appears in other and widely different species, it is not thought to have any phyletic significance.

Any supposed close phyletic relationship between *H. barbarae* and the other members of the paedophagous species group would also be difficult to substantiate. At present all that can be suggested is that *H. barbarae* might represent an isolated line, derived from a generalized and probably insectivorous stem, paralleling trophically the paedophagous species group (itself probably of diphyletic origin). Alternatively, *H. barbarae* might represent a survivor of the stem from which such species as *H. cryptodon* and *H. microdon* arose ; more will have to be learned about the anatomy of *H. barbarae* before this possibility can be substantiated.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.243	Napoleon Gulf, off Jinja . . .	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.5 (Holotype)	Beach near Nasu Point (Buvuma Channel) . . .	E.A.F.R.O.
	TANZANIA	
B.M. (N.H.) 1966.3.9.244–251	Beach near Majita . . .	E.A.F.R.O.

Haplochromis tridens Regan and Trewavas, 1928
(Text-fig. 20)

Haplochromis tridens Regan & Trewavas, 1928, *Ann. Mag. nat. Hist.* (10), **2**, 226.

LECTOTYPE : a fish 116·0 mm. standard length (caudal fin damaged), B.M. (N.H.) reg. no. 1928.6.2.41, collected in Tanzanian waters at Michael Graham's station 234 (1° 4′ S, 32° 13′ E), at a depth of over 100 ft. (Graham, 1929).

DESCRIPTION : based on 16 specimens (including the lectotype and the paralectotype) 72–119 mm. standard length.

Depth of body 30·1–36·2 (M = 33·5) per cent of standard length, length of head 32·0–37·2 (M = 35·4) per cent. Dorsal head profile straight, but interrupted by the prominent premaxillary pedicels, sloping steeply at 40°–45°. The cephalic lateral line system with prominent pores, especially those of the preopercular and preorbital canals. These pores are probably larger than in any Lake Victoria *Haplochromis* (including *H. pachycephalus* and *H. boops*).

Preorbital depth 16·0–20·9 (M = 17·2) per cent of head, least interorbital width 15·0–19·5 (M = 16·7) per cent. Snout 1·0–1·3 (mode 1·1) times as long as broad, its length 28·0–34·8 (M = 30·4) per cent of head. Eye with an oval, horizontally aligned pupil, eye diameter 25·6–34·0 (M = 30·7) per cent of head, depth of cheek 17·5–22·8 (M = 19·2) per cent.

Caudal peduncle 16·7–19·8 (M = 17·9) per cent of standard length, 1·4–1·9 (mode 1·6) times as long as deep.

Mouth horizontal or slightly oblique, lower jaw projecting slightly and with a distinct mental projection ; length of lower jaw 43·3–51·8 (M = 47·5) per cent of head, 2·0–2·8 (mode) times as long as broad. Premaxilla slightly expanded in the midline. Posterior tip of the maxilla generally reaching to below the anterior part of the eye, and occasionally to below the pupil ; rarely reaching only to the vertical through the anterior margin of the orbit.

Gill rakers : relatively slender, except for the lower 1–3 which are reduced, and the upper 2–4 which are usually flat ; 8–11 (mode 9) on the lower part of the first gill arch.

Scales : strongly ctenoid, especially those on the chest region. Lateral line with 31 (f.4), 32 (f.5), 33 (f.4) or 34 (f.2) scales. Cheek with 3 (mode) or 4 rows. Five and a half to 6½ (modes 6 and 6½) scales between the upper lateral line and the dorsal fin origin, 5–6½ (mode) between the pectoral and pelvic fin bases.

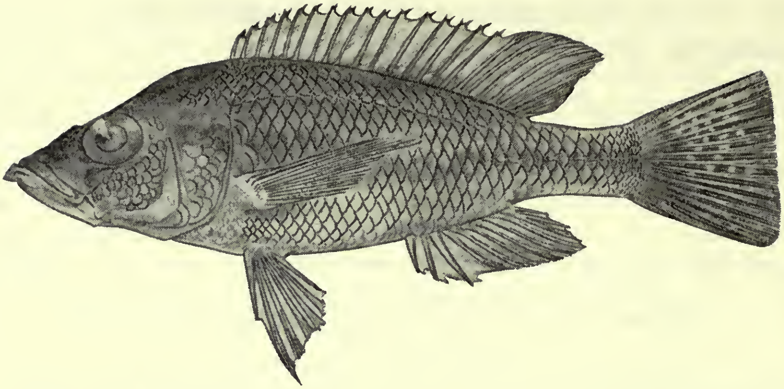

FIG. 20. *Haplochromis tridens*, paralectotype, about ·73 times natural size. Drawn by Miss M. Fasken.

Fins. Dorsal with 23 (f.7), 24 (f.7) or 25 (f.2) rays, comprising 15 (f.4) or 16 (f.12) spinous, and 7 (f.6), 8 (f.6), 9 (f.3) or 10 (f.1) branched rays. Anal with 10 (f.10), 11 (f.5) or 12 (f.1) rays, comprising 3 spines and 7 (f.10), 8 (f.5) or 9 (f.1) branched elements. (*N.B.* More than usual difficulty was experienced in deciding if the last dorsal and anal ray was a single, deeply divided element, or two distinct rays ; this may account for the number of specimens with low (7) branched ray counts). Pectoral 27·0–33·3 (M = 29·3) per cent of standard length. Pelvics with the first branched ray produced, proportionately more so in adult males. Caudal truncate.

Teeth. The trivial name "*tridens*" was given to the species because the larger of the two syntypes had only tricuspid teeth in the outer tooth row of both jaws, an unusual (probably unique) feature for a *Haplochromis* species. This condition is, however, rare in the species. Uni-, bi- and tricuspid outer teeth may all occur in a single specimen. Tricuspid teeth, at least in the upper jaw, are usually found posterolaterally, the bi- and unicuspids laterally and anteriorly. This arrangement is by no means constant ; in some specimens tricuspids occur anteriorly and anterolaterally. One fish (72 mm. S.L.) has only bicuspids in the upper jaw, and another (81 mm.) only unicuspids. There is no apparent correlation between the predominance of any one tooth form and the size of the fish. In three out of the sixteen specimens examined, no tricuspid outer teeth were found in either jaw.

There are 58–80 (M = 66) teeth in the outer row of the upper jaw.

Variation in the type of outer teeth occurring in the lower jaw follows the same pattern as in the upper jaw.

Teeth forming the inner rows in both jaws are predominantly tricuspids. These teeth are relatively large, are stout, and have the median cusp larger than the lateral ones. There are usually 2 inner rows (occasionally 3, rarely 4) in the upper jaw, and 2 (rarely 1) in the lower.

Osteology. No entire skeleton is available. The lower pharyngeal bone has its dentigerous surface equilateral or slightly broader than long. The lower pharyngeal teeth have cuspidate, compressed crowns, and cylindrical necks ; the teeth are arranged in 22–26 rows.

Vertebral counts in 10 specimens are: 13 + 16 (f.7) and 13 + 17 (f.3), giving totals of 29 and 30.

Coloration. Live colours are unknown. *Preserved specimens : Males* (*adult and sexually active*) : ground colour grey-blue (gun-metal) above the upper lateral line, greyish silver on the flanks, and light dusky silver on the chest and belly. Dorsal and caudal fins hyaline. Anal hyaline except for a dusky area between the spines, and black lappets ; the dusky area extends as a fairly distinct line at the base of the spinous part, and may be expanded basally onto the soft fin. There are two, large, grey-white anal ocelli. Pelvics dusky, darkest on the lateral four-fifths of the fin.

Males (adult but quiescent) have a ground coloration more like that of females. All fins are hyaline except for a faint darkening between the anal spines, and on the pelvic fins.

Females (*juvenile and adult*) : greyish silver above, shading to silver below. One specimen (ovaries ripening) is darker dorsally (almost brown), and has a broad, interrupted midlateral stripe running from behind the operculum to about half the length of the caudal fin (on which the stripe narrows) ; the band is interrupted at about the middle of its length. All fins yellowish to hyaline.

Ecology. Habitat. Excepting the two types, all the material came from one trawl haul at an unknown locality (thought to be off the Kenya coast). The types came from deep water (more than 100 ft.) some distance off-shore, and from over a soft bottom. The large eyes and hypertrophied pores of the cephalic lateral line system certainly suggest adaptations to a deepwater habitat.

Food. Only 6 of the 10 specimens examined (all from the same, and unknown, locality) contained ingested material in the gut. In each, the predominant contents are undigested blue-green algae, and empty diatom frustules. Two specimens have, in addition, a few fragments of Crustacea, and some unidentifiable insect remains.

Breeding. All fourteen of the non-typical specimens are adults. The types are not well-preserved internally, but both appear to be females.

Affinities. The admixture of tri-, uni- and bicuspid outer teeth together with the hypertrophy of the cephalic lateral line pores, provide a trenchant means of distinguishing *H. tridens* from other species in the lake. Indeed, it is difficult to suggest any close relationship between this species and any other so far considered. Perhaps some relationship will become apparent when more is known about the numerous and small species of *Haplochromis* which make up the bulk of fishes caught by trawling in the deeper waters of Lake Victoria (Greenwood, unpublished). Anticipating these results, it is possible to say that the elongate body and general " predatory " facies (especially the large mouth) of *H. tridens* are not common amongst these species, and nor is the *H. tridens* dental type.

Amongst the larger species with a predatory facies, *H. tridens* most closely resembles *H. victorianus*. There are, however, many differences between the species, not least of which are their differences in ecology and the much smaller adult size of *H. tridens*. *Haplochromis victorianus* differs also in its dentition, broader interorbital region (21·5–24·5, M = 22·6% of head, *cf.* 15·0–19·5, M = 16·7%) smaller and rounder eye (21·7–25·5, M = 23·6% head, *cf.* 25·6–34·0, M = 30·7%), and deeper cheek (22·5–26·2, M = 24·6% head, *cf.* 17·5–22·8, M = 19·9%). It should be remembered, however, that the data for *H. victorianus* are derived from larger specimens than are available for *H. tridens*, and that the most trenchant morphometric differences are in characters most affected by allometric growth. Nevertheless, it seems very unlikely that *H. victorianus* and *H. tridens* are close relatives.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	TANZANIA	
B.M. (N.H.) 1928.6.2.41 (Lectotype)	1° 04′ S, 32° 13′ E . . .	M. Graham
B.M. (N.H.) 1928.6.2.42 (Paralectotype)	1° 04′ S, 32° 13′ E . . .	M. Graham
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.152–165	Locality unknown (? Kenya coast)	E.A.F.R.O.

Haplochromis orthostoma Regan, 1922

(Text-fig. 21)

Pelmatochromis spekii (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 417.
Haplochromis orthostoma Regan, 1922, *Proc. zool. Soc. Londn.*, 184, fig. 9.

HOLOTYPE: a male (probably adult), 91 mm. standard length (B.M. [N.H.] reg. no. 1912.10.15.67) from Lake Salisbury (Kyoga system). The specimen is now in very poor condition, and has lost most of its scales.

This species, possibly one of the two most distinctive looking members of the Victoria-Kyoga flock, was described from a single specimen. Since then, two further specimens have been collected from Lake Salisbury, and three superficially similar specimens have been caught in Lake Victoria. The latter specimens differ from the Salisbury fishes in their dentition (and some other characters) and are thought to represent a distinct species. It is for this reason that I am redescribing the Lake Salisbury species in this paper.

The unusual physiognomy of *H. orthostoma* is well shown in text-figure 21; the snout and nuchal region meet at a distinct angle, the nuchal musculature not bulging anteriorly and laterally. Since there are only three specimens available, morphometric characters are tabulated below. The holotype is indicated with an asterisk.

S.L. (mm.)	Depth †	Head †	Preorb. %	Interorb. %	Snout %	Eye %	Cheek %	Caudal Peduncle†
67·5	37·0	36·0	19·6	20·4	32·7	24·5	24·5	19·3
83·0	35·0	36·1	20·0	23·3	30·0	21·7	30·0	17·5
*91·0	36·3	35·5	18·5	21·5	30·8	22·8	30·8	16·5

† Per cent of standard length.
% Per cent of head length.

Mouth very oblique, sloping at *ca* 50°–70°, the lower jaw projecting, its length 51·0–56·6 per cent of head length, and 2·5–3·4 times as long as broad. Lips not thickened, the lower jaw with a distinct mental protuberance. Posterior tip of the maxilla reaching a point about midway between the vertical through the anterior orbital margin and that through the nostril. Snout 1·1–1·3 times as long as broad, its dorsal surface slightly rounded, the premaxillary pedicels not prominent.

Caudal peduncle 1·5–1·6 times as long as deep.

Gill rakers : moderately stout, the lower 1–3 reduced, the upper 2 or 3 flattened (anvil-shaped in one fish) ; 9 or 10 on the lower part of the first gill arch (11 on one arch of a fish with 9 rakers on the other arch).

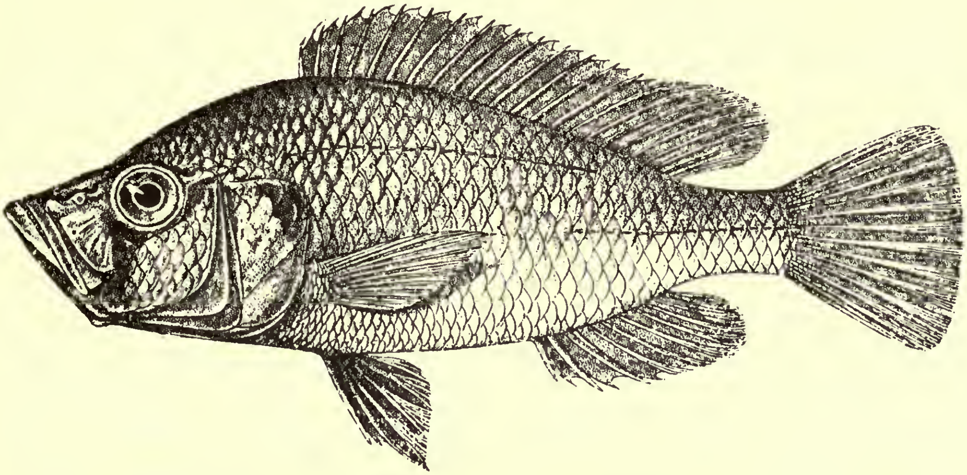

FIG. 21. *Haplochromis orthostoma*, holotype. From Regan, *Proc. zool. Soc.*, about ·86 times natural size.

Scales : ctenoid ; lateral line with 30 or 31 scales (Regan gives 33 for the now scaleless type), cheek with 3 or 4 rows (4 or 5 in the type according to Regan). Six or 6½ between the upper lateral line and the dorsal fin origin (6 or 7 in the type acc. Regan), 6 or 7 between the pectoral and pelvic fin bases, the chest scales small.

Fins. Dorsal with 14 (f.1) or 15 (f.2) spines and 9 branched rays, anal with 3 spines and 8 (f.2) or 9 branched rays. First branched pelvic ray not produced in the type, but elongate in the two other specimens (male and female). Caudal subtrucate.

Teeth. In the two larger specimens (83 and 91 mm. S.L.), the outer teeth in both jaws are a most distinctive feature. These teeth are slender and unicuspid with sharply curved tips directed medially ; those situated anteriorly are somewhat larger than the others. There are 66 and 61 teeth in this row for the two specimens respectively. In the lower jaw, the outer teeth, at least anteriorly, are somewhat stouter than their opposites in the upper jaw.

The smallest specimen (67·5 mm. S.L.) has outer teeth quite unlike those of the larger individuals. In the upper jaw, the anterior and lateral teeth are stout and bicuspid, those situated laterally and posteriorly are stout and tricuspid. All outer teeth in the lower jaw are bicuspid and stout, and are a little stouter than the upper jaw teeth. There are 68 teeth in the outer row of the upper jaw.

The inner teeth in the two larger fishes are unicuspid, small, slender and implanted obliquely; in the smallest fish they are small and tricuspid.

The dental arcade in all specimens is V shaped with a rounded apex; there are 2 inner tooth rows in the upper jaw, and 1 or 2 rows in the lower jaw.

Osteology. No complete skeleton is available. The lower pharyngeal bone has a triangular and equilateral dentigerous area. The teeth are relatively slender, with bicuspid and weakly compressed crowns, and are arranged in 20–22 rows; except in the smallest fish the teeth of the two median rows are coarser than the lateral rows.

Vertebral counts for 2 specimens are: 13 + 16 (type) and 12 + 16.

Coloration: Live colours are unknown. The type is now completely colourless; originally it was described as greyish, with a dark lachrymal stripe, and blackish pelvic fins. A juvenile female has a brown ground coloration, with very faint traces of four broad vertical bars on the flanks running from the dorsal fin origin to about the level of the ventral margin of the pectoral fin. No lachrymal stripe is visible. The lower jaw (especially over its anterior half) is rather dusky. The dorsal and caudal fins are yellowish, the former with black lappets. Anal dusky yellow. Pelvics faintly dusky, especially at their tips. Pectorals yellowish-grey.

Adult Male (probably fixed in alcohol): light brown above, shading to silver on the mid-flanks, and silvery white on the belly. Snout dark, as are the lips; branchiostegal membrane pale. A faint lachrymal stripe is visible. Dorsal fin greyish, with black lappets. Anal greyish, with two white ocelli. Caudal grey, the melanophores most concentrated along its midline. Pelvics dark along the anterior quarter, hyaline elsewhere.

Ecology. No information is available on the habitat or food of *H. orthostoma*, nor is there any information on the breeding habits of the species. The two males (91 and 83 mm. S.L.) are adult, and the female (67·5 mm.) is apparently immature.

Affinities. The peculiar head shape, large and very oblique mouth, coupled with the peculiar tooth form (at least in the larger fishes), serve to distinguish the species from all others in the Lake Victoria-Kyoga flock. The nearest relative is *H. parorthostoma* from Lake Victoria (see below). Further material, and field observations, may yet show that the two species are not distinct at that level.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
B.M. (N.H.) 1912.10.15.67 (Holotype)	Lake Salisbury	Presented by F. J. Jackson
B.M. (N.H.) 1958.12.5.173	Ongino, Lake Salisbury	Pitman
B.M. (N.H.) 1966.3.9.252	Lake Salisbury	E.A.F.R.O.

Haplochromis parorthostoma sp. nov.

(Text-fig. 22)

Holotype : an adult male, 117 mm. standard length, from near Zero Island (Buvuma Channel), Uganda. B.M. (N.H.) reg. no. 1966.2.21.4.

Description. The overall similarity between this species and *H. orthostoma* is great, particularly since both share a peculiar head profile not seen in any other *Haplochromis* species from Lakes Victoria or Kyoga.

The dorsal head profile is strongly concave, with the nuchal region meeting the snout at a noticeable but rounded angle, the junction emphasized by an anterior bulge of the cephalic epaxial body musculature. This muscular protuberance gives the fish a pronounced " forehead ", especially in the frontal plane.

Since only three specimens are available, morphometric data are tabulated below ; the holotype is marked with an asterisk.

S.L. (mm.)	Depth †	Head †	Preorb. %	Interorb. %	Snout %	Eye %	Cheek %	Caudal Peduncle†
86·0	38·4	35·0	16·7	20·0	31·6	27·7	25·0	17·5
110·0	42·3	36·4	17·5	17·5	33·8	25·0	27·5	12·7
*117·0	41·0	35·0	19·5	19·5	34·9	24·4	26·8	14·5

† Per cent of standard length.
% Per cent of head length.

Mouth oblique, sloping upwards at *ca.* 40°–50°, jaws equal anteriorly, or the lower projecting slightly. Lower jaw length 48·3–53·5 per cent of head, 2·3–2·4 times as long as broad ; chin with a distinct protuberance. Posterior tip of the maxilla reaching a point nearer the vertical through the anterior orbital margin than one through the nostril. Snout 1·2 times as long as broad, with a convex dorsal surface ; premaxillary pedicels not prominent. Lips moderately thickened.

Caudal peduncle 1·1–1·3 times as long as deep.

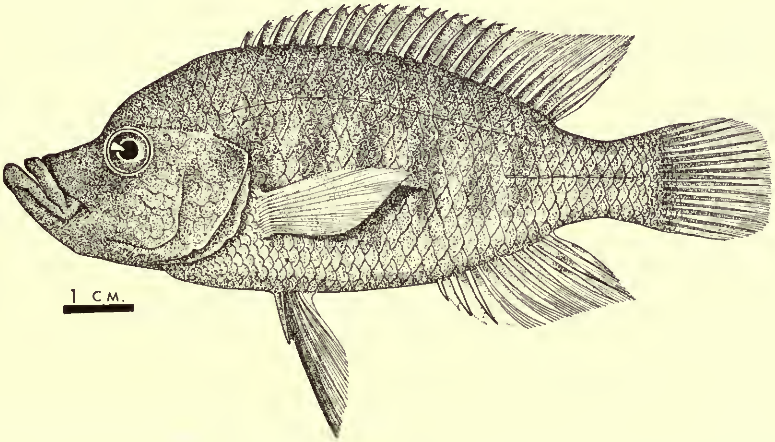

Fig. 22. *Haplochromis parorthostoma.* Drawn by Lavinia Beard.

Gill rakers : moderately stout (relatively stouter in one specimen), the lower 1–3 reduced, the upper 2 or 3 expanded and anvil-shaped ; 9 (f.2) or 10 rakers on the lower part of the first gill arch.

Scales : ctenoid, lateral line with 30 or 32 (f.2) scales, cheek with 2 or 3 rows (in the former specimen, the scales not covering the ventral aspects of the cheek). Six or 7 scales between the upper lateral line and the dorsal fin origin, 6 or 7 between the pectoral and pelvic fin bases.

Fins. Dorsal with 15 (f.2) or 16 spines and 8, 9 or 10 branched rays. Anal with 3 spines and 8 or 9 (f.2) branched rays, the spines short and stout. Pectoral 24·5–26·2 per cent of standard length. First branched pelvic ray not or slightly produced (all specimens are males). Caudal almost rounded, scaled on its basal two-thirds.

Teeth. The outer row in both jaws is composed of unicuspid, slender and slightly curved teeth, the curvature being gentle and not confined to the distal part of the tooth (*cf. H. orthostoma*, p. 101) ; in one fish, the last three teeth in the upper jaw are larger, stouter and straighter than the anterior ones. A few bicuspid, moderately stout teeth occur posteriorly in the lower jaw of the smallest (86 mm.) fish. In no specimen are the lower jaw teeth stouter than those in the upper jaw. There are 38, 40 and 52 teeth in the outer row of the upper jaw.

Teeth forming the inner series are small, tricuspid and weakly tricuspid, and are arranged in 3 or 4 rows in the upper jaws and in 2 rows in the lower.

The dental arcade is V shaped, with the apex broadly rounded.

Osteology. No complete skeleton is available. The lower pharyngeal bone has its triangular dentigerous surface as long as broad, or slightly broader than long. The teeth, arranged in 24–30 rows, are fine, with weakly compressed bicuspid crowns ; those in the two median rows are but slightly larger than the lateral teeth.

Vertebral counts in 3 specimens are : 13 + 15 and 13 + 16 (f.2).

Coloration : Live colours are known for a sexually active (but not ripe) *male*. Ground colour dark slate-grey, with faint vertical bars of a darker shade. Dorsal fin dark grey with crimson lappets on the posterior two-thirds of the spinous part, and a dark crimson margin to the entire soft part. Caudal dark grey with a crimson flush, particularly intense on its lower half. Entire anal fin, except for a dark base, crimson. Pelvics black on the anterior third, remainder dull crimson.

Preserved material : Males (adult). Ground colour light brown (including the branchiostegal membrane in two fishes ; this membrane blackish in the third specimen) ; flank crossed by 5 or 6 dark but incomplete bars, each bar originating just above the upper lateral line and extending to about the level of the ventral margin of the pectoral fin. A fairly distinct vertical lachrymal stripe runs from the anteroventral margin of the orbit to the angle of the lower jaw. Dorsal fin yellowish-brown along its margin, but dark brown between the rays. Anal yellowish, sooty or dark brown between the branched rays ; very faint indications of 2 or 3 whiteish ocelli. Caudal light to dark brown (almost black). Pelvics dusky on the anterior third to half, otherwise hyaline.

Ecology. One specimen came from an exposed, sandy beach, another from a rocky outcrop in about 20 ft. of water near an off-shore island, and the third from over a rocky shelf in about 40 ft. of water, also near an island.

No information is available on the food of *H. parorthostoma*. The three specimens are adult males.

Affinities. *Haplochromis parorthostoma* seems to be very closely related to *H. orthostoma* of the Kyoga system, at least in its peculiar head-shape. There is, however, a marked interspecific difference in the shape of the outer teeth. In *H. parorthostoma* these teeth are gently curved, whereas in *H. orthostoma* they have sharply recurved crowns but relatively straight necks. Furthermore, the inner teeth of *H. orthostoma* are unicuspid and arranged in one or two rows, but in *H. parorthostoma* are tricuspid and arranged in three or four rows in the upper jaw (two rows in the lower). An exception (at least with regard to outer tooth shape) is provided by the smallest specimen of *H. orthostoma* whose stout, erect and bicuspid teeth do not resemble those of its larger congeners (or, for that matter, *H. parorthostoma*). But, since the cranial morphology of this small fish is so like that of larger *H. orthostoma* individuals it is included in that species.

Haplochromis parorthostoma and *H. orthostoma* differ in characters other than dental ones. The bulging cranial epaxial muscles of *H. parorthostoma* impart a different shape to the dorsal head profile, which is further modified by the less oblique mouth. The available samples also suggest that *H. parorthostoma* has a bigger eye than *H. orthostoma* (and this despite the fact that the specimens of *H. parorthostoma* are larger) and probably a shorter and broader lower jaw.

Clearly, much more material is required before it will be possible to reach more definite conclusion about the status of the two species. Even then the decision will be complicated by the fact that they are allopatric, and their areas of distribution are physically isolated (now by the virtually impenetrable Owen Falls dam, and previously by the Ripon Falls, perhaps not a complete barrier to migration from Lake Victoria to the Kyoga system).

For the moment it is not possible to speculate on the wider relationship of these two species.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.) 1966.2.21 (Holotype)	Near Zero Island (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.253	Near Zero Island (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.254	Near Kazima Island . . .	Uganda Fish. Dept.

Haplochromis apogonoides sp. nov.

(Text-fig. 23)

HOLOTYPE an adult male, 118 mm. standard length, from Ekunu Bay, Uganda. B.M. (N.H.) reg. no. 1966.2.21.3.

Named " *apogonoides* " because of its fancied resemblance to the genus *Apogon*.

Description : based on eight specimens (including the holotype) 112–132 mm. standard length ; with one exception (a quiescent female) all are males.

Depth of body 36·0–39·6 (M = 38·1) per cent of standard length, length of head 35·0–37·2 (M = 36·1) per cent. Dorsal head profile curved (strongly so in some specimens), sloping fairly steeply (*ca.* 40°), the premaxillary pedicels not prominent.

Preorbital depth 13·6–16·7 (M = 15·2) per cent of head length, least interorbital width 27·5–31·0 (M = 29·5) per cent. Snout 1·3–1·5 (mode 1·4) times as broad as long, its length 29·3–33·4 (M = 31·2) per cent of head, eye 25·3–27·5 (M = 26·6), depth of cheek 27·8–31·0 (M = 29·3) per cent.

Caudal peduncle 15·3–19·8 (M = 18·0) per cent of standard length, 1·5–1·7 times as long as deep.

Mouth slightly to moderately oblique, lips somewhat thickened, the jaws equal anteriorly. Lower jaw 45·0–51·0 (M = 47·9) per cent of head, 1·2–1·5 (modal range 1·4–1·5) times as long as broad. Posterior tip of the maxilla reaching to below the pupil. Premaxilla not expanded medially.

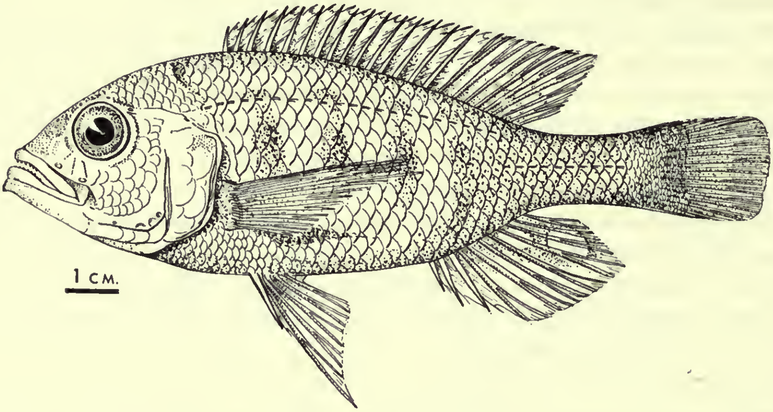

Fig. 23. *Haplochromis apogonoides.* Drawn by Barbara Williams.

Gill rakers : stout, the lower 1–3 reduced, the upper 3 or 4 flat ; 8–10 on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 32 (f.4), 33 (f.3) or 34 (f.1) scales. Cheek with 3 or 4 (mode) rows. Six to 8 (mode 6) scales between the upper lateral line and the dorsal fin origin, 6–8 (modes 6 and 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 22 (f.1), 24 (f.6), or 25 (f.1) rays, comprising 14 (f.2) or 15 (f.6) spinous and 8 (f.1), 9 (f.5) or 10 (f.2) branched rays. Anal with 10 (f.1), 11 (f.5) or 12 (f.2) rays, comprising 3 spines and 7 (f.1), 8 (f.5) or 9 (f.2) branched elements. Pectoral 29·0–34·1 (M = 30·8) per cent of standard length. Pelvics with the first ray slightly produced. Caudal truncate to subtruncate, scaled on its basal half to two-thirds.

Teeth. The outer teeth in both jaws are a characteristic feature of the species, being unicuspid, moderately stout and with very strongly recurved tips. Such teeth are otherwise found only in the *H. sauvagei* species group (see Greenwood, 1957). There are 50–60 (M = 58) teeth in the outer row of the upper jaw.

The inner teeth are also unicuspid, large and recurved, and are implanted obliquely. There are 2 rows in the upper jaw, and 1 or 2 rows in the lower jaw. A distinct space separates the inner series from the outer row.

Osteology. No complete skeleton is available. The lower pharyngeal bone is relatively stout, the dentigerous surface noticeably broader than long ($1\frac{1}{5}$ to $1\frac{1}{4}$ times). The teeth are stout and cuspidate, and are arranged in from 16–20 rows, those of the two median rows being slightly coarser than the others.

Vertebral counts in 7 specimens are : 13 + 15 (f.1), 13 + 16 (f.5) and 14 + 16 (f.1), giving totals of 28–30.

Coloration. Live colours are unknown. *Preserved coloration : Males (adult and sexually active, but probably not ripe).* Ground colour light yellow-brown, with a silvery underlay on the flanks. Belly, chest and branchiostegal membrane dusky, the branchiostegal membrane darkest below the opercular region. On the flanks there are faint traces of 4 or 5 fairly broad vertical bars which become very faint dorsally and ventrally ; the anterior 3 or 4 bars merge ventrally with the dark belly coloration. A dark lachrymal stripe is present ; it does not reach the ventral margin of the preorbital, but appears to pass upwards across the eye. Dorsal fin yellowish, the soft part maculate in some specimens ; also in some fishes the lappets are black. Caudal yellowish marginally and on the distal third to quarter, dark yellow-brown proximally. Anal yellowish, with one large greyish to whiteish ocellus faintly outlined in black. Pelvics sooty, the colour less intense between the last two or three rays.

Female (adult and quiescent). Ground colour greyish-silver. A very faint lachrymal bar extends from below the orbit to below the posterior tip of the maxilla ; a dark spot on the upper part of the eye suggests that this bar may pass across the eye. All fins are yellowish, the dorsal with dusky lappets, and the pelvics with a faint duskiness over the anterior rays.

Ecology. Habitat. The species has been caught in two localities only. In one, a sheltered bay, the water was between 20 and 30 feet deep, and the substrate of organic mud. The second locality was at a depth of about 80 ft in the Buvuma Channel, near Buvuma Island ; again the substrate (on which the nets were set) was organic mud.

Food. Regrettably, the gut was empty in all except one specimen ; this fish contained only a little, unidentifiable sludge.

Breeding. Apart from the sexually inactive female (132 mm. S.L.), all the specimens are adult and active males.

Affinities. The stout, unicuspid outer teeth with sharply recurved crowns immediately suggest affinity with *H. sauvagei*, *H. prodromus* and *H. granti* (Greenwood, 1957). Like these species, the dorsal head profile of *H. apogonoides* is strongly rounded. However, unlike these species, there are fewer rows of inner teeth in *H. apogonoides*, there is a distinct interspace between the inner and outer tooth rows, and the lower jaw is much longer (45·0–51·0, M = 47·9% head *cf.* 30·6–37·7, M = 34·5% for *H. sauvagei*, 30·5–37·8, M = 34·3% for *H. prodromus*, and 22·2–30·6, M = 26·8% for *H. granti*). *Haplochromis apogonoides* also differs from these species in its broader snout, and from *H. granti* in the anatomy of the jaws (see Greenwood, 1957).

Superficially, *H. apogonoides* resembles *H. cronus* (Greenwood, 1959) and, to a lesser degree, *H. empodisma* and *H. michaeli* (see Greenwood, 1960 and 1962 for the species respectively).

From *H. cronus*, it is differentiated by its dental morphology and its longer lower jaw.

From *H. empodisma*, *H. apogonoides* differs in its longer lower jaw (45·0–51·0, M = 47·9 per cent of head, *cf.* 39·1–48·7, M = 43·9%), dental morphology (strongly *cf.* gently curved teeth), broader interorbital (27·5–31·0, M = 29·5% head, *cf.* 20·6–28·6, M = 24·3), broader snout, and noticeably wider dentigerous surface on the lower pharyngeal bone($1\frac{1}{5}$–$1\frac{1}{4}$ times as broad as long, *cf.* longer than broad).

Haplochromis apogonoides differs from *H. michaeli* in dental morphology (see above), in its slightly deeper body, shallower preorbital, broader interorbital, markedly broader snout, and deeper cheek (27·8–31·0, M = 29·2% of head, *cf.* 22·9–27·7, M = 25·8%). The lower pharyngeal bone is similar in both species, but the teeth in *H. apogonoides* are stouter.

The marked similarity between the outer jaw teeth of *H. apognoides* and those in species of the *H. sauvagei* complex (which includes *H. xenognathus*, a species not mentioned above because of its distinctive jaw morphology, tooth pattern, and head shape) suggests that *H. apogonoides* might be an off-shoot from this species group. Unfortunately, nothing is known about the feeding habits of this species; all members of the *H. sauvagei* group are snail-eaters with the unusual habit of removing the snail from its shell before ingesting it. The large mouth and not especially strong jaws of *H. apogonoides*, do not, however, suggest similar feeding methods; rather, these characters indicate piscivorous habits.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.2.21.3 (Holotype)	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.238–242	Ekunu Bay	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.236–237	Locality unknown . . .	E.A.F.R.O.

DISCUSSION

Phylogeny

In an earlier paper (Greenwood, 1962) I outlined the various morphological trends shown by the piscivorous species, and suggested a possible ancestral morphotype (represented today by *H. brownae*) from which the different lines could have evolved. Also in that paper I indicated two major, and two minor, possibly phyletic groups of fish-eating predators. Additional information provided by the species described above does not affect the suggested trends, but does alter the phyletic picture. It now seems likely that there are three major phyletic lines, and probably three minor ones as well.

As mentioned before (Greenwood, *op. cit.*), possible phyletic lines amongst piscivorous species are less readily detected and defined than those of other trophic groups. In these latter there are dental as well as somatic characters which may be used for this purpose, but amongst the piscivores (at least when adult) the teeth are invariably unicuspid and of a very similar form. The principal " group " characters in these fishes are neurocranial shape, and body form ; the latter character often shows a greater or lesser degree of intergroup convergence. Using these two character complexes, I at first recognized two species aggregates, the " *serranus* " group, and the " *mento-macrognathus* " group. The former comprises the supposedly more generalized, broad-headed and deep-bodied species, and the latter group the more specialized, slender-bodied forms.

Information obtained from the species described in this paper suggests that my " *mento-macrognathus* " group consists of two groups, neither of which is as readily defined as the " *serranus* " group, but both being easily distinguished from that group.

One of the minor groups (that of *H. percoides*, *H. flavipinnis* and *H. cavifrons*) is now thought to be polyphyletic (see p. 113).

For convenience the groups will be referred to by the trivial epithet of a constituent species, which species, however, is not necessarily to be considered a " typical " member of the group. Indeed it is often difficult to determine just what a " typical " species would be ; at the most, the nominate species of a group is representative of a structural type found in three or four species of the group.

The three major groups are : (i) The " *serranus* " group, consisting of *H. serranus*, *H. victorianus*, *H. nyanzae*, *H. spekii*, *H. maculipinna*, *H. boops*, *H. thuragnathus* and *H. pachycephalus :* morphologically, this is a relatively homogeneous group (but, see also p. 110).

(ii) The " *altigenis* " group, comprising *H. guiarti*, *H. bayoni*, *H. dentex*, *H. pseudopellegrini*, *H. altigenis*, *H. pellegrini* and *H. dichrourus* ; a number of subgroups (some monotypic) can be recognized, and are discussed later.

(iii) The " *prognathus* " group, comprising *H. paraguiarti*, *H. acidens*, *H. prognathus*, *H. bartoni*, *H. estor*, *H. gowersi*, *H. mento*, *H. mandibularis*, *H. macrognathus*, *H. longirostris* and *H. argenteus*. This, the largest species aggregate shows several intragroup trends of which the most distinctive are the *H. longirostris*—*H. argenteus*, and the *H. mandibularis*—*H. macrognathus* subgroups.

Members of the " *serranus* " group differ from those of the other two groups in having shorter snouts* (one species out of seven with the snout $>$ 36 per cent of head length, *cf.* fourteen species out of eighteen), deeper bodies (one species out of seven with the body depth $<$ 36 per cent of standard length, *cf.* seventeen out of eighteen), and broader heads (no species with the interorbital width $<$ 22·6 per cent of head, *cf.* thirteen out of eighteen species.) Osteologically, the group is characterized by having a neurocranial shape nearest that of the generalized skull (see Greenwood, 1962), but with the preotic part elongate. The dorsal skull roof is straight and slopes fairly steeply, is broad both interorbitally and across the otic region, and the supraoccipital crest is high and presents a substantial area for muscle insertion (see fig. 25 in Greenwood, *op. cit.*).

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* The figures given are derived from those for the mean value of a particular character in species of the groups under consideration.

The " *serranus* " group could have evolved directly from an *H. brownae*-like ancestor, the principal morphological changes being an increase in adult size, and those alterations in neurocranial proportions already mentioned. Within the group, the most differentiated species are *H. boops*, *H. thuragnathus* and *H. pachycephalus*, all three being confined to deep water (see pp. 49, 50 and 41). *Haplochromis boops* and *H. thuragnathus* were apparently derived from an *H. maculipinna*-like ancestor, whilst *H. pachycephalus* seems to show greater affinity with the *H. serranus—H. spekii* level of organization. *Haplochromis maculipinna* is also essentially of this affinity, but has markedly larger eyes. In turn, *H. serranus* is clearly derived from an *H. brownae*-like stem.

The " *altigenis* " and " *prognathus* " groups probably evolved from an *H. guiarti*-like ancestor or ancestors, the latter species also showing affinities with *H. brownae*. Although both the " *altigenis* " and " *prognathus* " groups have included species with a relatively deep body, the main trend shown by both groups is towards a slender, somewhat compressed body-form and a correlated head shape. It is difficult to characterize these two groups, particularly their more basic members. The most trenchant group characters are probably in neurocranial form. In lateral view there is little to differentiate the skull form in the two groups ; both have the preorbital part relatively more elongate than in the " *serranus* "-type skull, the dorsal profile slopes upward at a rather slight angle (as compared with the angle in skulls of the " *serranus* " group), and the supraoccipital crest is relatively low. (These generalizations must, however, be modified somewhat for those species which seem to be structurally basal for the groups [*H. guiarti* and *H. pseudopellegrini* for the " *altigenis* " group, and *H. paraguiarti* and *H. acidens* for the " *prognathus* " group]. In these species the preorbital face is less protracted and consequently [since relative neurocranial depth varies little amongst all members of both groups] the dorsal skull roof slopes more steeply and the supraoccipital crest is higher and has a fairly extensive area). However, when the neurocranium is viewed dorsally, a difference between the groups (including their basal species) is apparent (see text-fig. 24). In members of the " *altigenis* " group, the otic region is relatively broader than in those of the " *prognathus* " group so that the outline narrows more rapidly (from a point immediately behind the orbit) than in " *prognathus* " skulls. In these the outline is that of a narrow wedge with the margins closing gradually from a point further behind the orbits. In supposedly basal members of both groups, the otic region is of about equal relative breadth but basal " *prognathus* " members nevertheless have a more gradual medial inclination of the lateral margins. Furthermore, in these species the dorsal skull profile is straighter than in the most basic " *altigenis* " group member, *H. guiarti*. Indeed, in most members of the " *altigenis* " group the profile is more curved than in species of the " *prognathus* " group.

Reasons for considering *H. guiarti* as a basic morphotype in the radiations of

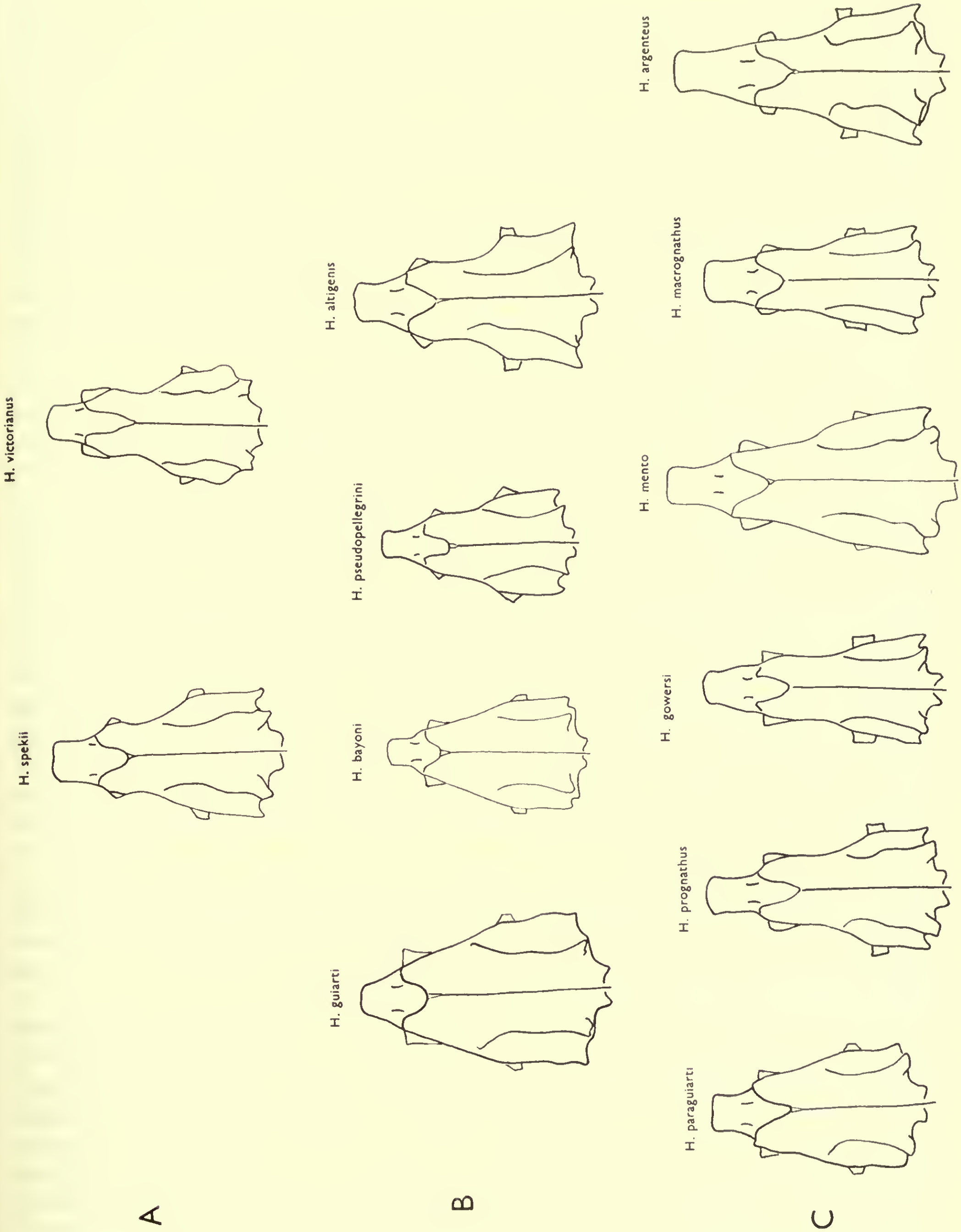
H. victorianus
H. spekii
H. altigenis
H. pseudopellegrini
H. bayoni
H. guiarti
H. argenteus
H. macrognathus
H. mento
H. gowersi
H. prognathus
H. paraguiarti
A
B
C

FIG. 24. Outlines of the dorsicranium in species of : line A, the " *serranus*-group ", line B, the " *altigenis*-group ", and line C, the " *prognathus*-group" .

predatory piscivores have been discussed already (see Greenwood, 1962). Starting from a species similar to *H. guiarti*, the principal morphological changes seen amongst species of the "*altigenis*" group involve relative elongation of the preorbital face, a slight decrease in skull height (especially in the otic region) and a consequent flattening in the slope of the dorsal skull profile. In these respects *H. bayoni* represents a fairly marked departure from the basic "*guiarti*" skull form, but one less marked than that shown by *H. dentex*, *H. altigenis* or *H. pellegrini*, particularly the latter (see fig. 25 in Greenwood, 1962). A link between these forms is provided by the skull of *H. pseudopellegrini* which is intermediate between the "*bayoni*" and "*altigenis*" types. There is not a great deal of difference in body form or jaw morphology among members of the "*altigenis*" group. Perhaps the most extreme member is *H. altigenis* itself, a species with the deepest head and consequently the largest mouth. *Haplochromis pellegrini* is, because of its small adult size and relatively small mouth, atypical for the group.

There is far greater variation in body form and cranial morphology within the "*prognathus*" group. Here the basic species, *H. paraguiarti* and *H. acidens*, are morphologically similar to *H. bayoni* of the "*altigenis*" group and could be derived either from a "*bayoni*" or a "*guiarti*"-like ancestor. *Haplochromis acidens* is, of course, peculiar in that despite its predatory facies, it is apparently a phytophage (see p. 76). *Haplochromis prognathus* and *H. bartoni* are, in most respects, very similar to one another and represent the next morphological step in the evolution of such species as *H. longirostris* and *H. mandibularis* from a "*paraguiarti*"-like stem. That is to say, the neurocranium clearly shows narrowing and elongation, and there is a related refinement of body proportions. *Haplochromis estor* and *H. gowersi* continue this trend with, in addition, the development of a more oblique angle to the jaws, and in *H. gowersi* a deepening of the cheek which contributes to a larger buccal cavity. *Haplochromis mento* probably evolved from a "*prognathus*"-like ancestor, and shows many of the trends exhibited by *H. gowersi* and *H. estor*. However, in this species the mouth is almost horizontal, and the neurocranium is somewhat nearer that of *H. prognathus*.

Also apparently stemming from a "*prognathus*"-like ancestor is *H. mandibularis*. Here the trend is towards further narrowing of the skull, deepening of the cheek, increased obliquity of the jaws and lengthening of the lower jaw. This trend culminates in *H. macrognathus* (see Greenwood, 1962, pp. 180 and 186), a species which could well be a direct descendant of *H. mandibularis*.

A third derivative from a "*prognathus*" or "*bartoni*"-like ancestor is *H. longirostris*. In this line there has been little change in neurocranial shape but there is a marked increase in jaw obliquity (much greater, too, than in the "*mandibularis*"-"*macrognathus*" line), and a marked refinement in body proportions which results in one of the most slender bodies found amongst Lake Victoria *Haplochromis* species. These characters are shared by *H. argenteus*, although the elongate body-form seems less obvious in that species. *Haplochromis argenteus* could be derived either from a "*longirostris*"-like stem, or perhaps directly from a "*prognathus*"-like ancestor.

Thus, the "*prognathus*" group seems to show at least three radiations from a basal "*prognathus*"–"*bartoni*" stem, *viz.* the *H. estor*, *H. gowersi*, *H. mento* sub-group, and the *H. mandibularis–H. macrognathus*, and *H. longirostris–H. argenteus* species pairs (but see above for possible reservations about the last named pair). It seems reasonable to assume that the *H. prognathus* level of organization was derived from a level similar to that shown by the extant species *H. paraguiarti*. The relationships of that species are, however, less clear-cut. As was mentioned above, *H. paraguiarti* shows several structural affinities with *H. bayoni*, a species probably derived from an *H. guiarti*-like ancestor. But, it is difficult to overrule the possibility that *H. paraguiarti* evolved independently from an *H. brownae*-like stem. (The status of *H. brownae* in relation to the piscivorous predators is discussed in Greenwood, 1962).

Two species, *H. plagiostoma* and *H. xenostoma*, have not been included in the discussion so far. Both are characterized by having the mouth set at a very steep angle to the horizontal (*ca.* 40°–50°) ; *H. plagiostoma* is further characterized by its obliquely truncate caudal fin, and *H. xenostoma* by its pronounced prognathism. Because of these characters, especially the oblique jaws, neither species shows any obvious superficial similarity with members of the groups discussed above. The neurocranium of *H. plagiostoma* is of the "*serranus*" type (see also Greenwood, 1962) but also shows certain "*guiarti*"-like features. Thus, on this character complex *H. plagiostoma* could either be associated with the "*serranus*" group or be looked upon as an isolated offshoot of the "*altigenis*" group arising from an ancestor near the stem of that complex. In either eventuality, *H. plagiostoma* is not linked with the basal group by any extant, structurally intermediate species.

Haplochromis xenostoma, both in its overall organization and in its neurocranial form, seems to represent a further development from a "*plagiostoma*" stem. The chief trend involves an increase in adult size, and a relative enlargement of the mouth and jaws. The neurocranium of *H. xenostoma* reflects these changes, especially in the longer preorbital region ; it is thus essentially a "*serranus*" group neurocranium. From the available evidence it is impossible to determine whether *H. plagiostoma* and *H. xenostoma* are part of the same phyletic lineage or whether the two species are end-points of parallel evolution from "*guiarti*" and "*serranus*"-like stems respectively.

The two smaller species complexes, the *H. michaeli*, *H. martini*, *H. squamulatus* group and the *H. percoides*, *H. flavipinnis*, *H. cavifrons* group, will now be considered.

The relationships of *H. michaeli* and *H. martini* are discussed in my paper of 1962, and there is nothing further to add. *Haplochromis squamulatus* is included with these species because of its several similarities with *H. martini*, similarities which include a basically similar coloration of a type not otherwise found in species of the Lake Victoria *Haplochromis* flock. In the "*michaeli*" group, the relationship between *H. martini* and *H. squamulatus* seems to be closer and more direct than that between either species and *H. michaeli* (see also Greenwood, 1960, pp. 245–8 ; *idem*, 1962, p. 206, and p. 91 above).

When discussing the relationships of the *H. percoides–H. cavifrons* group (Greenwood, 1962), I suggested that *H. percoides* could have evolved from an *H. pellegrini*-like stem, and that *H. flavipinnis* was a derivative of an *H. percoides*-like ancestor. Also in that paper I noted the less certain relationships of *H. cavifrons*, but considered it to be part of the *H. percoides* phyletic line. On revising this complex, I began to doubt my earlier conclusions about the affinities of *H. cavifrons*, which now seems to have greater relationship with the "*serranus*" group. This review provided no evidence to negative my conclusions about the interrelationships of *H. percoides* and *H. flavipinnis*, or the association of *H. percoides* with an *H. pellegrini*-like ancestor. However, I am not at all certain about the validity of my previous suggestion that the neurocrania of *H. percoides* and *H. flavipinnis* show affinity with those of *H. bartoni* and *H. longirostris* (i.e. with the "*prognathus*" group as it is now defined). With a better appreciation of neurocranial form in the piscivores as a whole, I now think that the skull of *H. percoides* is basically an "*altigenis*" group one, as is the skull of *H. pellegrini*.

Similar re-evaluation leads me to think that the syncranial organization and form shown by *H. cavifrons* links that species more closely with the "*serranus*" group than with the "*altigenis*" group and its *H. percoides*-like off-shoots. The freckled coloration of *H. cavifrons* remains unique (Greenwood, 1962), and nothing approaching it is seen in the "*serranus*" group. If *H. cavifrons* is a "*serranus*"-group derivative, then it stands in the same relationship to that group as does *H. plagiostoma*, namely as an isolated off-shoot without any extant intermediates bridging the gap.

Thus, the *H. percoides–H. cavifrons* "group", although a valid one on grounds of general similarity between the constituent species, is probably polyphyletic in origin.

Because so little material or information is available on three species described above (*H. tridens*, *H. orthostoma*, and *H. parorthostoma*), they cannot as yet be included in a discussion on phylogeny. *Haplochromis tridens* does not seem to be related to any of the piscivorous species groups; its affinities probably lie with the complex of small, bottom-living species which form the bulk of trawl catches in sheltered, mud-bottomed areas of the lake. *Haplochromis orthostoma* and *H. parothostoma* are closely related to one another but cannot readily be associated with any other species.

Leaving for the moment those species which as adults feed on post-larval fishes, consideration will be given to species which prey on larval and embryo fishes, the paedophagous species. Only one paedophage, *H. barbarae*, is described in this paper; the others are dealt with in an earlier publication (Greenwood, 1959).

Haplochromis barbarae resembles small specimens of *H. guiarti* and adults of *H. brownae*, and does not show any close similarity in body form, jaw morphology or dentition with other paedophagous species; unfortunately it has not been possible to study its osteology in detail. The probable phylogeny of the larval and embryo fish eating species was discussed in the paper cited above; the conclusion reached was that the group had a polyphyletic origin. Little more can be added to these thoughts, except to reconsider the possible relationships existing between *H. parvidens* and *H. acidens* (previously misidentified as *H. nigrescens*; see above, p. 73). The morphology of the lower jaw in *H. parvidens* differs considerably from that of *H. acidens* (as does the diet, paedophage *cf.* herbivore); but, in other syncranial characters, and in body-form, the species are very similar. In these latter characters the two species are more similar than are *H. microdon* and *H. cryptodon*, the only known paedophages showing a morphotype which could be ancestral to that of the "*parvidens*" level. *Haplochromis cryptodon* could have evolved from an *H. brownae*-like stem (possibly one like *H. barbarae* which had already adopted paedophagous habits?), the chief morphological changes involving the dentition (reduction), jaw form (to give greater distensibility) and a differential growth of the preorbital neurocranium (also leading to greater jaw motility). The changes in neurocranial form would lead to a skull essentially like that found in basal species of the "*altigenis*" and "*prognathus*" groups, in other words one like that in *H. acidens*. Thus, the origin of the "*parvidens*" structural grade is equivocal.

Reconsidering the relationship of this grade (as represented by *H. cryptodon*, *H. parvidens* and *H. microdon*) with the other distensibly-mouthed grade of paedophages (represented by *H. obesus* and *H. maxillaris*), I can find, as before, few reasons to support a close phyletic linkage between them. Osteologically neither *H. obesus* nor *H. maxillaris* has a dentary like that occurring in the *H. parvidens* group, nor in the case of *H. obesus* is its form one from which a "*parvidens*" type might evolve. The neurocranium of *H. obesus* is most unlike that of the "*parvidens*" group, but that of *H. maxillaris* is virtually identical with the skull of *H. cryptodon*. The character which most clearly distinguishes these two species from any member of the "*parvidens*" group is the occurrence of teeth in which the crowns are curved labially (and not buccally as is usual in unicuspid teeth). This dental character is so marked, and restricted to these two species, that I am inclined to give it considerable weight when speculating on phylogenies, particularly since this tooth-form seems to have no adaptive significance. If the peculiar teeth in *H. maxillaris* and *H. obesus* do indicate a fundamental relationship between the species, then their syncranial differences would suggest an independent origin from a common stem, possibly a form like *H. cronus* (see Greenwood, 1959). Dentally, and also in its general level of organization, *H. cronus* is like those generalized *Haplochromis* species that attain a larger adult size than most members of that group ; it could be derived from an *H. empodisma*-like stem (see Greenwood, 1960).

Natural History

Only broad generalizations can be made about the natural history of the piscivorous predators. To date, seventy-nine species of Lake Victoria *Haplochromis* (and related monotypic genera) have been revised. Of these, forty-two species can be classed as piscivores, thirty-four species preying on free-swimming fishes, and eight species on cichlid embryos and larvae presumably taken from the mouths of parent fishes. Anticipating results still to be obtained from those species as yet unanalyzed, it seems probable that the number of non-piscivorous species will be increased substantially. I suspect that ultimately the number of piscivorous species will be about forty per cent of the total. These figures apply to sub-adult and adult members of the species only since no data are available on the feeding habits of younger stages. The same restrictions apply to considerations on habitat preferences among the piscivores.

Piscivorous species have been found in all the localities so far sampled, but much of the deeper water in Lake Victoria remains unexplored, especially at the levels occupied by bathypelagic species. In order to give a general picture of habitats in the lake, these can be divided, rather crudely, into three types: (i) sheltered areas such as bays and the smaller gulfs. (ii) Exposed areas, especially wave-washed beaches. (iii) Relatively undisturbed, open, off-shore waters (undisturbed that is, relative to the rather turbulent conditions prevailing over exposed beaches), not enclosed in gulfs or bays. Such a subdivision is, in many respects, unsatisfactory because conditions like those in habitat (iii) do occur in the larger gulfs and bays.

More species are found in sheltered areas (habitat [i]) than in the other two habitats; 23 species have been recorded frequently in habitat (i), 14 from habitat (ii), and 15 from habitat (iii), with, in the habitats respectively, 2, 3, and 1 species occurring infrequently. However, these various species are by no means confined to a particular habitat. For example, 11 species were found in both sheltered and exposed areas, 9 in sheltered and off-shore habitats (3 of these species also occurring over beaches); only 6 species are apparently confined to sheltered areas. Two species occur both over beaches and in the quieter off-shore areas, and only 4 are apparently confined to the latter habitat (but 3 of these species are known only from deep water). The nature of the substrate seems to exert a less restricting influence on the piscivores than on members of other trophic groups. Twenty-four species are recorded as occurring over hard substrata (sand, shingle or rock), and 20 over a soft substrate (organic mud); 10 of these species are found over both kinds of substrate, 6 are thought to be confined to a soft bottom, and 13 to a hard substrate.

The eight strictly paedophagous species (see Greenwood, 1959, and p. 114 above) are not included in the analysis above. These species appear to be rather more restricted in their distribution, particularly from the viewpoint of depth range. It seems that the paedophages are confined to the littoral and immediately sublittoral zone, and are probably restricted to sheltered bays and exposed beaches.

The depth range of the other 34 piscivores is, in general, confined to water less than 60 ft. deep (with of course, the exception of *H. boops*, *H. pachycephalus*, *H. thuragnathus* and *H. dichrourus* which have been caught in water about 120 ft. deep). Most species have a wide range within these depth limits, and few if any are restricted to purely littoral areas. However, it must be emphasized that this picture may be unduly biased by sampling limitations. The horizontal distribution of the species has not been studied critically; in water less than 20 feet deep, the spatial distribution of piscivores caught in nets set to cover about the first five feet of water below the surface, and the five feet above the bottom, does not show any obvious horizontal stratification of the particular species. But, these observations were not tested statistically.

From the relatively few gut analyses available it would seem that the majority of piscivores prey on other *Haplochromis* species, and to a much lesser extent on small cyprinid fishes (especially *Engraulicypris argenteus*). Some species have a mixed insect-fish diet, and there are several records of otherwise exclusively piscivorous species eating insects when these are periodically and suddenly super-abundant, as for instance after a heavy termite hatch. The paedophagous species appear to feed mostly on cichlid embryos and larvae (it is presumed those of *Haplochromis* species), but insects are also recorded from the gut contents of these species.

Information on the breeding habits of piscivores is almost non-existent ; in those cases where some data are available, the species are known to be female mouth brooders. The turbidity of the water in most parts of Lake Victoria has precluded field observations on the actual spawning sites of both predators and prey alike.

There has not yet been enough collecting on a lake-wide basis to establish whether or not any of the fish-eating species has a geographically restricted distribution. For eight species this possibility can definitely be overruled, (and in ten others it seems very unlikely) but for sixteen species there are suggestions of geographical restriction because they have not been caught in some regions where, on the basis of habitat and niche suitability, they should be present.

SUMMARY

(1) Ten species are redescribed on the basis of new material.

(2) Nine new species (*H. pachycephalus*, *H. boops*, *H. thuragnathus*, *H. pseudopellegrini*, *H. paraguiarti*, *H. acidens*, *H. barbarae*, *H. parorthostoma* and *H. apogonoides*) are described.

(3) Although all these species have a general facies and dentition usually associated with piscivorous habits, some do not belong to this trophic group ; one species (*H. acidens*) is apparently herbivorous.

(4) The possible phyletic interrelationships of the piscivorous species are discussed. Three major morphological groups can be detected, at least on the basis of their more extreme members, but the boundaries are ill-defined. Some minor groups are also considered, as are the larval and embryo fish-eating species groups.

(5) Broad summaries of the natural history of piscivorous species are given.

(6) The holotype of *Astatotilapia nigrescens* Pellegrin is redescribed and its possible synonymy discussed.

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Through the cooperation of Dr. M. Blanc of the Paris Museum, I have been able to examine Pellegrin's type specimens and thus to settle several problems. Dr. Paul Kahsbauer of the Vienna Museum has graciously lent me Lohberger's type material ; I am deeply indebted to him for this privilege.

In east Africa, Dr. M. Gee and Mr. R. Welcomme of E.A.F.F.R.O. aided my studies by proving additional material and field observations ; material collected by the Uganda Fisheries Department has provided many specimens from localities which I was unable to sample personally. The cooperation of E.A.F.F.R.O. and the Uganda Fisheries Department is warmly appreciated.

APPENDIX

The disputed identity of *Astatotilapia nigrescens* Pellegrin, 1909, (*Bull. Soc. Zool. France*, **34**, 157) was mentioned on page 73. Boulenger (1915) synonymized this species with *Haplochromis percoides* Blgr. 1906. Regan (1922), however, resurrected the species as *Haplochromis nigrescens,* and included in his redescription a number of specimens which I have placed in a new species, *H. acidens*. Pellegrin's figure of *A. nigrescens* is misleading and does not convey an accurate impression of the holotype and unique specimen (Paris Museum, number 09–508).

Recently, I examined this specimen, an immature male 71 mm. standard length, collected by Alluaud from the Kavirondo Gulf, Kenya. It does not agree closely with any other specimens I have handled, but is does show affinity with both *H. percoides* Blgr., 1906 and *H. flavipinnis* (Blg.), 1906, especially the latter.

Before considering its identity further, a redescription of the holotype will be given.

	mm.	Proportional percentage
Standard length	71·0	
Depth of body	24·0	33·8 standard length
Length of head	26·0	36·6 standard length
Depth of preorbital	4·3	16·5 head length
Width of interorbital	6·0	23·1 head length
Length of snout	8·0	30·8 head length
Diameter of eye	7·0	27·0 head length
Depth of cheek	6·5	25·0 head length
Length of lower jaw	12·0	46·2 head length
Length of caudal peduncle	13·0	18·3 standard length
Length of pectoral fin	18·0	25·3 standard length

Caudal peduncle 1·4 times as long as deep.

Lower jaw slightly oblique and very slightly projecting ; twice as long as broad. Posterior tip of the maxilla almost reaching the vertical through the anterior orbital margin.

Gill rakers : moderately stout, 9 on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 31 scales, cheek with 4 rows (the rows short, so that the anterior part of the cheek is naked). Seven scales between the upper lateral line and the dorsal fin origin ; 7 between the pectoral and pelvic fin bases. Chest, belly and nuchal scales small.

Teeth : in the outer row of both jaws relatively slender, slightly curved ; about 50 in the upper jaw. Inner teeth tricuspid or weakly tricuspid, arranged in 2 and 1 rows in the upper and lower jaw respectively.

Coloration. The preserved colour pattern (in shades of brown) closely resembles that of *H. percoides* and *H. flavipinnis* (see Greenwood, 1962). The dorsal fin is marbled, and the caudal both marbled and maculate ; the pelvics are dark.

Discussion : In its general facies, and particularly its head shape, the holotype of *A. nigrescens* resembles both *H. percoides* and *H. flavipinnis,* especially the former because the angle of the mouth is less oblique than in most specimens of *H. flavipinnis.* However, when morphometric characters are considered a number of differences between *H. percoides* and *A. nigrescens* holotype are apparent. In six characters (body depth, preorbital depth, interorbital width, snout length, eye diameter, and caudal peduncle length) the values fall outside the known range for *H. percoides*, and the lower jaw is relatively longer than in specimens of *H. percoides* of a comparable size.

There is greater correspondence between these characters in *A. nigrescens* and *H. flavipinnis*, since only two (the shallower preorbital and larger eye) fall outside the range for *H. flavipinnis*, but there is a greater difference in head shape.

Thus, *A. nigrescens* could be an aberrant specimen of either *H. flavipinnis* (differing especially in head shape) or *H. percoides* (numerous morphometric differences).

For the time being, however, I do not think that *A. nigrescens* can be formally synonymized with either species. I would prefer to recognize it as the purely nominal species *Haplochromis nigrescens* (Pellegrin) until more is known about the range of variation in small specimens of *H. flavipinnis*, the species I think it most closely resembles.

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THE VACHELL COLLECTION OF CHINESE FISHES IN CAMBRIDGE

P. J. P. WHITEHEAD & K. A. JOYSEY

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ZOOLOGY Vol. 15 No. 3
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BY

P. J. P. WHITEHEAD
(British Museum, Natural History)

and

K. A. JOYSEY
(University Museum of Zoology, Cambridge)

Pp. 121–165 ; 3 *Plates*

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THE VACHELL COLLECTION OF CHINESE FISHES IN CAMBRIDGE

By P. J. P. WHITEHEAD & K. A. JOYSEY

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ABSTRACT

The Rev. G. Vachell of Macao presented about a hundred Chinese fishes to the Cambridge Philosophical Society in the early part of the last century. In his *Report on the Ichthyology of the Seas of China and Japan,* Richardson based 22 new species on Vachell material. Although 80 species are listed here, the greater part of the Vachell collection is no longer extant and only 15 specimens survive ; these include the types of *Anguilla clathrata* Rich., *Pelor tigrinum* Rich., and *Seserinus vachellii* Rich.

1. INTRODUCTION

SOME 18th and 19th century fish collections are well-known and their contents well documented. Others have lapsed into obscurity and provide considerable difficulties when the need arises to establish types or validate old names. One of these is the Vachell collection of Chinese fishes, the remains of which are housed in the University Museum of Zoology in Cambridge.

The Vachell collection, which appears to have contained about 80 species of fish from Macao, formed a significant part of the material on which Sir John Richardson based his " Report on the Ichthyology of the Seas of China and Japan " published in 1846. As often happens with old collections, the Vachell material included a large proportion of types. Thus 22 of the new species described by Richardson in the " Report " were based on Vachell fishes. Unfortunately, only a fraction of the Vachell collection is now extant. But this collection is of sufficient importance for a complete list to be given, particularly in order to record those specimens which survive (including the types of 3 Richardson species) those which are missing (including 7 types), and those specimens which are now known with certainty to have been destroyed (including 12 types).

The principal author, P.J.P.W., is responsible for all the systematic zoology, and K.A.J. undertook the investigation of the records in Cambridge.

2. RICHARDSON'S "REPORT"

Richardson (1846) listed 665 species of fishes from the seas of China and Japan, an enormous increase on any previous list ; 142 of these were described as new species or varieties. Over three hundred of the species listed were represented by an original coloured drawing from a collection of illustrations of fishes from Macao and Canton compiled by John Reeves (1774–1856), an Inspector of Tea for the East India Company at Canton ; 83 new species introduced by Richardson were based solely on a Reeves illustration. Three sets of these illustrations are now in the Zoology Library of the British Museum (Natural History).

Since half (40 out of 80) of the species listed here (including 11 of the types) are illustrated by a Reeves drawing, the Reeves illustration number is cited in the synonymies. This may assist in identifying some of the missing Vachell specimens. The illustrations of the types are reproduced here, apparently for the first time (except *Chatoessus maculatus*—see Whitehead, 1966).

John Reeves, and his son J. R. Reeves, also sent a collection of fishes from Macao and Canton to the British Museum. These were examined by Richardson and Günther, and since they came from the same area as the Vachell fishes, reference is made to them in the text.

Richardson evidently examined the Vachell collection in the years up to 1845. Four of the species listed here (*Balistes vachellii*, *Anguilla clathrata*, *Aploactis breviceps*, and *Congrus lepturus*) had already been described as new by Richardson in the " Zoology of the Voyage of H.M.S. Sulphur " published in three parts between 1844 and 1845 (see " Report " p. 316 for dating). In general, however, Richardson left description of the Vachell material until the " Report ".

3. THE VACHELL COLLECTION

According to Richardson's " Report " (1846, p. 189), the Rev. George Vachell was Chaplain to the India Company at Macao in about 1830. He made a collection of about a hundred fishes from that region, and these were presented to the Philosophical Institution in Cambridge, preserved in spirits, and mostly in good condition. Nonetheless, Richardson himself described at least one fish as " not in very good condition " (p. 204), another that " the colours have suffered from long maceration in spirits " (p. 208), and another that " it is flaccid and may have lost its exact shape " (p. 267).

In 1865 the collections of the Cambridge Philosophical Society were transferred to the University of Cambridge and housed in the newly built Museum of Comparative Anatomy and Zoology. Indeed, the Philosophical Society Collection formed the nucleus of the Museum of Zoology, and although under the same roof as the Museum of Comparative Anatomy, the two collections were kept in separate rooms and remained distinct for several years. In 1867 J. W. Clark, who was Superintendant of the Museums, reported that, " Two presses have been provided to contain the collections of Fishes presented by the Philosophical Society. These consist of the following : the series of Fishes of Madeira, collected by Mr. Lowe, many of which are unique, and nearly all the types of his descriptions in the transactions of the Cambridge Philosophical Society : a considerable number of specimens procured by Mr. Darwin during the voyage of the ' Beagle ', also the types of the descriptions published by the late Sir John Richardson : a collection sent from China by Mr. Vachell ; and a collection of Fishes of Great Britain formed by the late Professor Henslow and Mr. L. Jenyns. These will at no distant period be named and catalogued by Dr. Günther, of the British Museum, who has most generously offered to undertake this work ". (It should be noted that the punctuation of this passage suggests that Clark did not realize that the Richardson types were included within the Vachell collection.)

The following year Clark (1868) reported that during 1866–67 " Dr. Günther, of the British Museum, one of the first ichthyologists in Europe, has been so kind as to examine the collections of Fish in spirits, and to determine those that were unnamed." The major part of Günther's " Catalogue " had by then been published, but Günther makes only rare reference to specimens in Cambridge in the subsequent volumes (7 and 8), and no mention at all of having seen Vachell fishes. It is probably for this reason that the Vachell collection has been generally ignored.

A few years later, Clark (1871) again referred to the identification of the spirit collection of Fish, Amphibia and Reptiles and reported that, " I had hoped to have announced the completion of an arrangement by which the services of Dr. A. Günther, of the British Museum, the best living authority on the subject, might have been secured for this work ; but though the proposal made by the Museums' Syndicate to the Trustees of the British Museum was a most liberal one, that body did not think proper to accede to it. It will therefore be necessary to select some other competent person ". Apparently this statement had the desired effect and only a year later Clark (1872) reported that these collections had been examined and determined by Dr. Günther! It is clear that in both 1866–67 and 1870–71, Günther worked on the fish collections in Cambridge. Shipley (1913) even claims (p. 265) that the fishes were catalogued by Dr. Günther, but we have been unable to trace any other record of such a catalogue, either in London or in Cambridge.

In 1893, S. F. Harmer catalogued the entire fish collection at Cambridge, indexing the species according to the volume and page numbers of Günther's " Catalogue". The names used by Harmer are generally identical to those of Günther, but in the case of the Vachell specimens the names often differ from those given in Richardson's " Report ". This suggests that Günther re-identified and relabelled many of the Vachell specimens, despite the fact that he did not refer to them in the " Catalogue ".

Altogether, 80 species (plus 3 names here considered synonyms) are listed as appearing either in Richardson's " Report " or in Harmer's catalogue, and often in both. The vast majority are now either missing or known to have been destroyed.

A total of 32 species which were listed by Richardson as including Vachell specimens are not so listed by Harmer (including the types of 10 Richardson species). These specimens may have been lost, exchanged or destroyed without record either in the Cambridge Philosophical Institute between 1845 and 1865, or in the Museum of Comparative Anatomy and Zoology between 1865 and 1893. It is possible that Richardson worked on some of the Vachell material at the British Museum, that it was never returned to the Philosophical Institution, and that it became incorporated into the British Museum collections without ever being registered. There are in fact a number of unregistered bottles, including some labelled as presented (or collected) by Richardson. In some cases these involve Vachell species which were never included in Harmer's Catalogue of Cambridge material, and each of these have been carefully checked. Unfortunately in no case is there supplementary evidence which would prove the case either way.

It is also known that J. W. Clark spent a good deal of the summer of 1866 overhauling the Physiological Series, which had just been moved into the newly built Museum in Cambridge, and it is recorded that useless and decayed specimens were thrown away (Clark, 1867; Shipley, 1913). Although this activity does not refer explicitly to the fish collection it does give a clear indication of the policy that was being implemented in the Museum during the same period that Günther was working on the fish, and this might account for some of the 32 species which were missing before Harmer's 1893 catalogue.

The possibility that some of the Vachell material was acquired by the British Museum between 1865 and 1893 has also been checked. Such an acquisition seems most likely to have occurred during or after Günther's visit in 1866–67, or as a part of the arrangement made in 1870–71, the terms of which are not known. But the British Museum registers from 1866–93 show no gifts, purchases or exchanges involving the Cambridge Museum. It is certain that no Vachell material went to London officially, and in some doubtful cases the British Museum material has been checked and no evidence found that any arrived unofficially.

Conversely, there are 16 species listed by Harmer as being Vachell material which are not so mentioned by Richardson. Either Richardson missed these, or perhaps they were not true Vachell specimens but were erroneously included by Harmer. Among these, one Cambridge specimen of *Boleophthalmus campylostomus* (see p. 147) was transferred to the British Museum in 1917, but although Harmer lists it as a Vachell fish, Richardson (Report, p. 209) states that he had seen no specimens.

Harmer's 1893 catalogue is in two parts, one listing the stored material and the other listing those specimens which were on exhibition at that time, the latter being given separate registration numbers. A large number of Harmer's entries in the catalogue of stored material have since been crossed out, and these specimens are no longer extant. A note in the front of the catalogue states: " The collection of fishes in store was overhauled during May, 1939, when specimens thought to be of little or no value were discarded." We understand from the present Director, Dr. F. R. Parrington, that this clearance included many dried-up, rotten and disintegrated specimens, and he recalls that his predecessor, Sir Clive Forster-Cooper, once recounted that some of the fishes which had matured beyond repair were found to have been pickled in rum! It seems certain that those specimens which are crossed off Harmer's catalogue were destroyed, in contrast to those which are just missing insofar as they do not appear in Harmer's list.

It is right and proper to ask why so little of the Vachell collection survives today, despite the fact that it was presented to an Institution which could well have been expected to provide security. Only by such enquiry can it be hoped to avoid similar disappointments in the future. In this case, there seems to have been a combination of circumstances. Richardson provides some evidence of poor fixation and preservation, which continued to take its toll more than a century later. Clark apparently did not appreciate that the Vachell collection included the Richardson types, and for some inexplicable reason Günther drew no attention to them. Hence, in the majority of cases, Harmer was unaware of the type specimens, and did not indicate them as such when he prepared his catalogue. In consequence, when the collection was overhauled nearly 50 years later, many types were discarded.

Until relatively recently it has been accepted practice in most museums that material which had suffered beyond repair was destroyed and crossed off the catalogue, unless, of course, it was recorded as type material. In retrospect this policy is to be regretted in the present case, and this has caused us to give some thought to the problem. For one reason or another, whether it be faulty fixation, poor storage conditions, sheer neglect or genuine accident, nearly all Museums possess some important material that has suffered, apparently beyond repair. We now hold the view that those responsible for such collections must accept this as almost inevitable, and without shame should retain such material, rather than totally destroying it. Advances in technology are now providing new methods of obtaining information from such material, and although apparently useless to one generation, it may be capable of yielding information to the next. Methods now exist for reconstituting dried up specimens, and for " developing " labels which have become illegible in ordinary light. In the present instance, X-ray photography of even the rotten material might have yielded sufficient information about the skeleton to establish the identity of the species, but unfortunately none of these techniques can now be applied, because most of the material has been destroyed.

4. SYSTEMATIC LIST

In the following list of Vachell species, the synonyms of Richardson and Günther have been given, headed by the modern name for the species. The latter have posed considerable difficulties, particularly when no specimens survive and where the identification must be made on a brief description by Richardson, sometimes supplemented by a Reeves illustration. Richardson's specimens were evidently not always consistent with the Reeves drawing (e.g. in the case of *Sebastodes vachellii* —p. 140), a fact not always appreciated by later authors. In many cases, therefore, it has been possible to do no more than to follow the comprehensive synonymies of Chu (1931), Herre (1953), Chu, Tchang & Chen (1964) and Fowler (*Synopsis of fishes of China*, from 1930 onwards) ; only Chu and Fowler have listed all or almost all Richardson names. Sometimes, a recent study of a particular group has helped to identify the Vachell material, but even then the Vachell specimens themselves do not appear to have been examined, perhaps since the time of Günther's visits to Cambridge nearly a century ago. In addition, very few authors seem to have examined the Reeves illustrations.

We have listed here fifteen specimens representing eleven species which appear to be part of the original Vachell collection. Even these numbers are by no means certain since several are listed only by Harmer and not by Richardson as being Vachell material. Notes on these extant specimens and their identifications are given separately in Section 5 (p. 147).

Those of Richardson's species which were based wholly or partly on Vachell material are marked with an asterisk and are listed separately in Table I.

We are particularly grateful to Mr. W. L. Chan, of the Fisheries Research Station in Hong Kong, for his help in identifying the fishes shown in the Reeves illustrations reproduced here and his comments on the Chinese names applied to these fishes.

Class *CHONDRICHTHYES*

Family **ORECTOLOBIDAE**

1. ***Chiloscyllium plagiosum*** (Bennett)

Chiloscyllium plagiosum: Richardson, 1846: 194 (Vachell material) (Reeves illustr. No. 252).
Chiloscyllium indicum: Günther, 1870, **8** : 413 (material listed under six varieties).

As *Chiloscyllium indicum* " (several) China Rev. G. Vachell " in Harmer's list—destroyed, 1912 according to catalogue. A half-grown Richardson specimen and a Reeves juvenile in British Museum. Günther does not mention any specimens in Cambridge, although he had inspected the Vachell material by this time. The identification of the three sharks listed here is based on the review of Taiwan species by Chen (1963).

Family **CARCHARHINIDAE**

2. ***Carcharhinus melanopterus*** Quoy & Gaim.

Carcharias (*Prionodon*) *melanopterus:* Richardson 1846: 194 (not stated as Vachell specimen) (Reeves illustr. No. 23).
Carcharias melanopterus: Günther, 1870, **8** : 369 (South Africa and Amboyna material only).

As *Carcharias* (*Prionodon*) *melanopterus*, juvenile " China, Rev. G. Vachell " in Harmer's list—destroyed. No Cambridge material mentioned by Günther.

Family **TRIAKIDAE**

3. ***Triakis scyllia*** Müller & Henle

Triakis scyllium: Richardson, 1846 : 195 (no specimens).
Triacis scyllium: Günther, 1870, **8** : 384 (no specimens).

As *Triacis ? scyllium*, juvenile, " China Rev. G. Vachell " in Harmer's list—destroyed. Vachell specimen presumably overlooked by Richardson, if indeed it did belong to the Vachell collection. Again, Günther makes no mention of Cambridge material.

Class *OSTEICHTHYES*

Family **CLUPEIDAE**

4. ***Clupanodon thrissa*** (Linnaeus)

**Chatoessus maculatus* Richardson, 1846 : 308 (a single Vachell specimen, TYPE) (Reeves illustr. No. 109).
Chatoessus maculatus: Günther, 1868, **7** : 409 (Formosa specimens only).

Harmer lists " *Clupea thrissa*. (several). No histy.", but these were subsequently destroyed. Since *Chatoessus maculatus* was the only clupeid represented in the Vachell collection, it is possible that one of the Harmer specimens was the type. Günther mentions only three Formosan specimens but not the Vachell material in Cambridge. For identification of *C. maculatus*, see Whitehead (1966). Reeves illustration reproduced here (Plate 1, fig. 1).

Family ENGRAULIDAE

5. ***Coilia playfairii*** (McClelland)

Coilia playfairii: Richardson, 1846 : 309 (see note below).
Coilia clupeoides: Günther, 1868, **7** : 404 (" Chinese Seas ", no mention of Cambridge material).

Listed as *Coilia* (*mystus*), with the name *clupeoides* written above, " ' Fishes from China ' Canton ", not in Harmer's hand—EXTANT. A single specimen now exists, but with only a modern label indicating that it is a Canton fish. However, Richardson states " specimens exist in all the collections of Chinese fishes that we have seen ". Günther does not mention having seen any Cambridge material. Measurements and notes on the extant specimen are given in Section 5 (p. 149), and further notes on Richardson material are given by Whitehead (1966).

Family SALANGIDAE

6. ***Salanx chinensis*** (Osbeck)

Leucosoma chinensis: Richardson, 1846 : 303 (Reeves and Vachell specimens).
Salanx chinensis: Günther, 1866, **6** : 205 (China, including type of *Leucosoma reevesii* Gray).

Listed by Harmer as " *Salanx chinensis* (2) ?History "—destroyed. The British Museum has a specimen from the Haslar collection, as well as the type of *Leucosoma reevesii.* Identification based on Chu (1931).

Family ANGUILLIDAE

7. ***Anguilla japonica*** (Temminck & Schlegel)

**Anguilla clathrata* Richardson, 1844 : 104 (one Vachell specimen, TYPE) ; *Idem,* 1846 : 312.
Anguilla clathrata: Günther, 1870, **8** : 23 (doubtful species No. 4, name only).

A single specimen listed by Harmer as *A. vulgaris* " China. Rev. G. Vachell."—EXTANT. This specimen was subsequently transferred as F.2002 to the Exhibited series. Günther had already examined the Vachell collection but did not acknowledge having seen this fish. Richardson's description (*Zoology of the Sulphur*, p. 104) was based on a Vachell fish of 8·8 inches from Canton. See Section 5 for description and notes on this HOLOTYPE.

Family MURAENESOCIDAE

8. ***Muraenesox cinereus*** (Forsskål)

Congrus tricuspidatus: Richardson, 1846 : 312 (Vachell specimens).
Muraenesox cinereus: Günther, 1870, **8** : 46 (Reeves specimens and type of *C. tricuspidatus*).

Listed as *M. cinereus* " China Rev. G. Vachell " by Harmer—destroyed. Cambridge material not mentioned by Günther. Identification based on Chu, Tchang & Chen (1963).

Family **CONGRIDAE**

9. ***Uroconger lepturus*** (Richardson)

Congrus lepturus Richardson, 1844 : 106, and 1846 : 132 (Canton, but no reference to Vachell specimens).

Uroconger lepturus: Günther, 1870, **8** : 44 (Reeves specimens, the TYPE, and another Chinese specimen).

Listed as *Uroconger lepturus*, 2 specimens " China Rev. G. Vachell " by Harmer—destroyed. Günther does not refer to Cambridge material. The species was described by Richardson (*Zoology of the Sulphur*, p. 106, Pl. 56, figs. 1–6) with a single set of measurements relating to a specimen of 9 inches from Canton, but no indication of the collector (presumably Reeves). There is a specimen of 160 mm. S.L. (10¼ inches) labelled as type in the British Museum (unregistered but with a metal tag " 821 ") ; the second Chinese specimen is even larger (322 mm.). The first is labelled "Reeves " and the second was purchased from a Mr. Warwick. Present identification based on Chu, Tchang & Chen (1963).

Family **OPHICHTHIDAE**

10. ***Pisodonophis boro*** (Ham. Buch.)

Ophisurus harancha: Richardson, 1846 : 313 (one fish of 14½ inches in Camb. Phil. Inst., a Reeves specimen and an Indian specimen).

Ophichthys pallens: Günther, 1870, **8** : 61 (the Reeves type only).

Harmer listed 2 specimens of *Ophichthys cancrivorus* " China Rev. G. Vachell "—destroyed. Although Richardson (1846) believed the Vachell, Reeves, and Indian specimens to be conspecific, he elsewhere (*Erebus & Terror*, p. 10) proposed the name *pallens* for the Reeves fish, while still claiming the Vachell specimen to be true *harancha*. Günther (1868, p. 61) considered Richardson's *harancha* to be *pallens*, as also did Chu (1931). Fowler (1932*a*, p. 126) agreed, but placed both under an earlier Hamilton-Buchanan name, *Pisodonophis boro*, and this course has been adopted here.

Family **BAGRIDAE**

11. ***Pseudobagrus vachellii*** (Richardson)

**Bagrus vachellii* Richardson, 1846 : 284 (one Vachell specimen of 5 inches, the TYPE).

Pseudobagrus vachellii: Günther, 1864, **5** : 85 (Chinese specimens).

Listed as *P. aurantiacus* " China. Rev. G. Vachell " in Harmer's catalogue—destroyed. Günther had kept the closely related *P. vachellii* and *P. aurantiacus* separate, but he may have reconsidered this when he came to identify the Cambridge material. Since Harmer listed two Vachell *Pseudobagrus* species, and Richardson two Vachell *Bagrus* species, it must be assumed that the two species correspond. Present identifications follow Chu (1931).

12. *Pelteobagrus fulvidraco* (Richardson)

**Bagrus limbatus* Richardson, 1846 : 283 (one Vachell specimen, the TYPE).
Pseudobagrus fulvi-draco: Günther, 1864, **5** : 85 (one Chinese fish presented by Günther himself).

Listed as *Pseudobagrus fulvi-draco* " China. Rev. G. Vachell " by Harmer—destroyed. Fowler (1932*b*) identified Richardson's species as *Plotosus anguillaris* (Bloch), but curiously did not list Richardson's *B. vachellii.*

Family **PLOTOSIDAE**

13. *Plotosus anguillaris* (Bloch)

Plotosus lineatus: Richardson, 1846 : 286 (specimens in the Camb. Phil. Inst.) (Reeves illustr. No. β11).
Plotosus anguillaris: Günther, 1864, **5** : 24 (Chinese specimens).

Listed as *Plotosus anguillaris* " (several) ?history " in Harmer's Catalogue—destroyed. Possibly the Cambridge Philosophical Institution had other Chinese material in addition to the Vachell specimens. Present identification based on Chu (1931) and Fowler (1932*b*).

Family **BELONIDAE**

14. *Strongylura strongylura* (van Hasselt)

Belone caudimaculata: Richardson, 1846 : 264 (no Vachell material) (Reeves illustr. No. β33).
Belone caudimaculata: Günther, 1866, **6** : 245 (no China specimens).

Listed as *B. strongylurus,* " ? China " by Harmer—destroyed. Richardson gave no description but mentioned specimens from Canton (Reeves) and from Port Essington. Günther (1866) placed the former in *B. strongylurus* and the latter in *B. caudimaculata.* Present identification based on Fowler (1932*b*).

Family **SOLEIDAE**

15. *Microbuglossus ovatus* (Richardson)

**Solea ovata* Richardson, 1846 : 279 (a single Vachell specimen, 3½ inches, the TYPE) (no Reeves illustr.).
Solea ovata: Günther, 1862, **4** : 472 (Chinese specimens).

Listed by Harmer under *Solea ovata,* 4 specimens " China Rev. G. Vachell "—destroyed. Günther (1862) lists an Amoy and a Haslar Collection specimen, and 4 fishes presented by Belcher. The latter are labelled as types, but they are too small and Richardson mentions only Vachell material. The single Haslar fish, however, may well have been 3½ inches in length (caudal now damaged) but there are 59 dorsal rays (65 described). Identification based on Chu, Tchang & Chen (1963).

16. ***Zebrias zebra*** (Bloch)

**Solea ommatura* Richardson, 1846 : 279 (two Vachell specimens, the TYPES) (Reeves illustr. No. β13).
Synaptura zebra: Günther, 1862, **4** : 484 (Chinese specimens).

Listed by Harmer, as *Synaptura zebra*, four fishes, " No histy."—destroyed. No British Museum material which could be the lost Vachell types. Reeves illustration reproduced here (Plate 1, fig. 4). Identification follows Chu, Tchang & Chen (1963).

Family **CYNOGLOSSIDAE**

17. ***Cynoglossus grammicus*** (Richardson)

**Plagiusa grammica* Richardson, 1846 : 280 (two Vachell specimens 3¾ inches, the TYPES) (no Reeves illustr.).
Plagiusa grammica: Günther, 1862, **4** : 492 (doubtful species No. 5, name and reference to the " typical specimen " in Camb. Phil. Soc. collection).

Listed as *Cynoglossus trigrammus* " (several). China. Rev. G. Vachell " by Harmer (presumably having been re-identified by Günther)—destroyed. No evidence of Vachell material in British Museum. Richardson's species is ignored by Chu, Tchang & Chen (1963), and the present identification follows Fowler (1934).

Family **HOLOCENTRIDAE**

18. ***Holocentrus ruber*** (Forsskål)

Holocentrum albo-rubrum: Richardson, 1846 : 223 (Vachell specimens) (Reeves illustr. α19.)
Holocentrum rubrum: Günther, 1859, **1** : 35 (Reeves and other Chinese material).

Two specimens are given in Harmer's list as *Holocentrum rubrum*, " China. Rev. G. Vachell."—EXTANT. There are also two dry specimens listed by Harmer but stated to have " no history ". These are also extant and were presumably identified by Günther. See Section 5 (p. 151) for notes on the two extant spirit specimens.

Family **CHANNIDAE**

19. ***Channa maculata*** (Lacepède)

Ophicephalus maculatus: Richardson, 1846 : 251 (two Vachell specimens) (Reeves illustr. Nos. 148 and β19).
Ophiocephalus maculatus: Günther, 1861, **3** : 480 (Reeves and China specimens).

Listed as *O. argus* in Harmer's list, 2 + 1 specimens, " China. Rev. G. Vachell "—destroyed. Günther considered *O. maculatus* to be close to *O. argus*, but seems to have re-identified the Cambridge material as the latter. Present identification based on Chu (1931).

Family ATHERINIDAE

20. *Atherina bleekeri* (Günther)

Atherina bleekeri Günther, 1861, **3** : 398 (Reeves specimens).

Listed as *A. bleekeri* " China. Rev. G. Vachell " by Harmer—destroyed. No species of *Atherina* are listed by Richardson, so Harmer's specimens were either overlooked or were not in fact Vachell fishes.

Family MUGILIDAE

21. *Mugil cephalus* (Linnaeus)

Mugil japonicus: Richardson, 1846 : 247 (no Vachell material).
Mugil cephalus: Günther, 1861, **3** : 419 (Reeves and Chinese specimens).

Listed as *M. cephalotus* by Harmer, 2 specimens " China. Rev. G. Vachell "—destroyed. Richardson included seven species of *Mugil* in the " Report ", none based on Vachell specimens. Richardson's *M. macrolepidotus* is another synonym of *M. cephalus*, according to Fowler (1935), who has been followed here.

Family SPHYRAENIDAE

22. *Sphyraena obtusata* (Cuvier)

Sphyraena chinensis: Richardson, 1846 : 266 (one Vachell specimen) (Reeves illustr. No. 62).
Sphyraena chinensis: Günther, 1860, **2** : 334 (doubtful species No. 1).

Not listed by Harmer. No British Museum specimens labelled *S. chinensis*. Present identification follows Chu (1931).

Family TRICHIURIDAE

23. *Lepturacanthus savala* (Cuvier)

Trichiurus intermedius: Richardson, 1846 : 268 (one British Museum specimen, but no Vachell material) (Reeves illustr. No. β56).
Trichiurus savala: Günther, 1860, **2** : 347 (East Indian and Chinese specimens).

One specimen listed by Harmer, as *T. muticus* " China. Rev. G. Vachell ", now transferred to Exhibited Series No. F.2685—EXTANT. Richardson placed *T. muticus* Gray in his synonymy of " *T. lepturus, japonicus* " (" Report ", p. 268), a record which he based solely on *T. lepturus* Temm. & Schl. from Japan. He included *Trichiurus savala* Cuvier in his synonymy of *T. armatus* Gray, but did not list any material at Cambridge. The present specimen may have been one that he overlooked. See Section 5 (p. 152) for discussion of this specimen.

Family **NOMEIDAE**

24. ***Psenopsis anomala*** (Temm. & Schl.)

**Trachinotus melo* Richardson, 1846 : 270 (one Vachell specimen, the TYPE) (Reeves illustr. No. 97).
Trachinotus melo: Günther, 1860, **2** : 485 (on Richardson's description, no specimens).

Not included in Harmer's list, presumed lost before 1893. The specimen is not in the British Museum collections. Reeves illustration reproduced here (Plate 1, fig. 3). Identification follows Chu (1931) and Fowler (1936).

Family **FORMIONIDAE**

25. ***Parastromateus niger*** (Bloch)

**Seserinus vachellii* Richardson, 1846 : 273 (two Vachell specimens, the larger 3·75 inches, the TYPES).
Stromateus niger: Günther, 1860, **2** : 401 (one Reeves specimen).

Harmer lists two specimens under the name *Platax teira* " China. Rev. G. Vachell." —EXTANT. These specimens have been identified as the types of *Seserinus vachellii*. See Section 5 (p. 153) for description and notes.

Family **CARANGIDAE**

26. ***Alectis indica*** (Rüppell)

Gallichthys major: Richardson, 1846 : 271 (one Vachell specimen) (Reeves illustr. No. 189).
Caranx gallus: Günther, 1860, **2** : 455 (one Reeves specimen and one other Chinese specimen).

As *Caranx gallus* in Harmer's catalogue, two fishes " China. Rev. G. Vachell "—destroyed. Identification follows Fowler (1936, p. 297), who used Cuvier's generic name *Scyris*.

27. ? ***Alectis ciliaris*** (Bloch)

Blepharis fasciatus: Richardson, 1846 : 271 (one Vachell specimen) (Reeves illustr. No. 269).
Blepharis fasciatus (*non* Rüpp.): Günther, 1860, **2** : 422 (doubtful species No. 19, typical specimen in Camb. Phil. Inst.).

Not listed by Harmer, presumed lost before 1893. Richardson identified his specimen with *B. fasciatus* Rüppell, a synonym of *A. ciliaris* (Bloch), but Günther disagreed (1860, p. 454), presumably on Richardson's description. Not in British Museum collections. Tentative identification of Fowler (1936, p. 295) followed here.

28. ***Caranx*** (***Atule***) ***kalla*** (Cuvier)

**Caranx cancroides* Richardson, 1846 : 274 (one Vachell specimen, the TYPE) (Reeves illustr. No. β30).
Caranx cancroides: Günther, 1860, **2** : 422 (doubtful species No. 12).

Not mentioned in Harmer's list, presumed lost or destroyed before 1893. Reeves illustration reproduced here (Plate 1, fig. 2). W. L. Chan (*in litt.*) states that in Hong Kong the vernacular name *Ha-tsee* on the Reeves illustration (*Hwa tsze* in the " Report ") refers (prefix) to shrimp, and (suffix) to " a carangid fish either typically of the genus *Decapterus*, or of the subgenus *Atule* Jordan." *Decapterus* can be ruled out as being too slender (depth about 5 or more times in total length ; about 3 in Richardson's description and in the drawing). *Caranx* (*Atule*) *kalla* Cuv. is the most likely species and one that is caught in fair numbers by the Hong Kong shrimp trawlers. Richardson states " No spots are shown on the operculum " (present in *C. kalla*), but the figure shows a fish of only 4½ inches.

29. ***Caranx malabaricus*** (Bloch & Schneider)

Caranx malabaricus: Richardson, 1846 : 275 (two Vachell specimens) (Reeves illustr. No. β21).
Caranx malabaricus: Günther, 1860, **2** : 436 (one Reeves and one other Chinese specimen ; BMNH. 1851.12.27.118).

Not listed by Harmer, presumed destroyed or lost before 1893. An unregistered specimen merely labelled " *Caranx malabaricus* " in British Museum collection, but no indication of donor. Identification based on Fowler (1936, p. 293), who placed the species in *Carangoides*.

30. ***Citula armata*** (Forsskål)

Caranx ciliaris: Richardson, 1846 : 276 (" spec. C. Ph. Inst.").
Caranx armatus: Günther, 1860, **2** : 453 (one Chinese specimen, BMNH. 1851.12.27.129, no donor given).

Listed by Harmer as *Caranx armatus* " China. Cambridge Philosoph. Society's Collection "—Extant, Exhibited Series No. F.2755. There is also an unregistered British Museum specimen with an old label " *Caranx ciliaris* " amended to " *armatus* ". The jar is unusual, being oval in cross-section and sealed with parchment ; such jars were initially suspected of being part of the Vachell collection, but the present case shows this to be incorrect. The Cambridge specimen is discussed further in Section 5 (p. 154).

Family **LEIOGNATHIDAE**

31. ***Leiognathus brevirostris*** (Valenciennes)

Equula nuchalis: Richardson, 1846 : 276 (two Vachell specimens) (Reeves illustr. Nos. G90 and β85).
Equula nuchalis: Günther, 1860, **2** : 500 (Reeves and other Chinese specimens).

Not included in Harmer's list. Reeves illustration No. β 85 is not a leiognathid, but No. G 90 is almost certainly *L. brevirostris*, having a distinct black pre-dorsal blotch, a body depth 2 1/5 times in S.L., and the lateral line not reaching the base of the caudal. Richardson gives no description.

Family **GERRIDAE**

32. ***Gerres erythrourus*** (Bloch)

Gerres equula: Richardson, 1846 : 239 (one Vachell fish) (Reeves illustr. No. 215).
Gerres oyena: Günther, 1859, **1** : 352 and 1862, **4** : 261 (no Chinese specimens).

Not included in Harmer's list. Identification follows Chu (1931).

Family **AMBASSIDAE**

33. ***Ambassis commersonii*** (Cuvier)

**Ambassis vachellii* Richardson, 1846 : 221 (one Vachell specimen, the TYPE) (no Reeves illustr.).
Ambassis vachellii: Günther, 1859, **1** : 227 (no British Museum specimens).

Listed as *Ambassis commersonii,* " ? China Rev. G. Vachell " in Harmer's catalogue, two specimens—destroyed. Fowler (1937) tentatively recognized Richardson's species because of its deep body, but without specimens or illustration the species must remain doubtful.

Family **SERRANIDAE**

34. ***Epinephelus fario*** (Thunberg)

Serranus trimaculatus: Richardson, 1846 : 232 (Vachell specimens).
Serranus trimaculatus: Günther, 1859, **1** : 109 (Reeves fish and another Chinese specimen).

As *S. trimaculatus* " China. Rev. G. Vachell " in Harmer's catalogue—destroyed, with date 21.4.1939. Identification based on Chu (1931) and Fowler (1938*a*, p. 273).

35. ***Epinephelus akaara*** (Temm. & Schl.)

**Serranus shihpan* Richardson, 1846 : 231 (Vachell specimens, also Reeves and Hyde Park collections all part of TYPE SERIES) (Reeves illustr. No. 71).
Serranus diacanthus: Günther, 1859, **1** : 110 (Chinese specimens, presented by Reeves, Richardson and the East India Co.).

Not included in Harmer's list. Günther placed Richardson's species in the synonymy of *S. diacanthus.* There are several unregistered Chinese specimens in the British Museum (including a Reeves fish) labelled *S. diacanthus,* but none labelled *S. shihpan.* Reeves illustration reproduced here (Plate 2, fig. 1).

Richardson was strongly inclined to refer this species to *E. akaara,* but decided to keep it separate because of the " dark bars which cross the body ". Matayama (1960), Chu, Tchang & Chen (1963), as well as earlier authors, have placed Richardson's species in the synonymy of *E. akaara,* but Fowler & Bean (1930) placed it in the synonymy of *E. malabaricus* (Bloch & Schn.). W. L. Chan (*in litt.*) has pointed out that the vernacular name *Sek-dang-paan* is used in Hong Kong for one of the commonest species, *E. fasciatomaculatus* (Peters), whereas *E. akaara* is known as *Hung-pan.* Also, the absence of definite spots on the dorsal fin in the Reeves figure, and the inclination of the vertical bars on the flanks and their tendency to fork ventrally, all point to *E. fasciatomaculatus*. However, Matayama (*loc. cit.*) placed *E. fasciatomaculatus* (Peters) as a synonym of *E. fario* (Thunberg), but considered *E. fasciatomaculatus* of Fowler & Bean to have been *E. diacanthus* (Val.). Because of such uncertainties in the nomenclature we have preferred to let Richardson's species remain in the synonymy of *E. akaara* for the time being.

Family **PRIACANTHIDAE**

36. ***Priacanthus tayenus*** (Richardson)

**Priacanthus tayenus* Richardson, 1846 : 237 (one Vachell specimen and one Reeves specimen, the TYPES) (Reeves illustr. No. β14).
Priacanthus tayenus: Günther, 1859, **1** : 221 (a single specimen, collected by Reeves).

Listed as *P. japonicus* " China. Rev. G. Vachell " by Harmer—destroyed. A single Reeves specimen in British Museum (BMNH. 1965.8.12.50) labelled as type. No evidence that the Vachell specimen is present. Reeves illustration reproduced here (Plate 2, fig. 2). Identification follows Chu (1931) and Fowler (1938*b*, p. 67).

Family **PEMPHERIDAE**

37. ***Pempheris otaitensis*** (Cuvier)

Pempheris otaitensis: Günther, 1860, **2** : 508 (one Chinese specimen).

Listed by Harmer as *P. otaitensis* " China. Rev. G. Vachell "—destroyed. Richardson (p. 244) only mentions the related *P. moluca* Cuvier without reference to any specimens at all.

Family **LUTJANIDAE**

38. ***Lutjanus erythropterus*** (Bloch)

Mesoprion annularis: Richardson, 1846 : 229 (one Vachell specimen).
Mesoprion annularis: Günther, 1859, **1** : 204 (Reeves specimens).

Two specimens included in Harmer's list as *M. annularis* " ? History "—destroyed. Identification follows Chu (1931) and Fowler (1938*b*, p. 83).

Family **POMADASYIDAE**

39. ***Pomadasys argenteus*** (Forsskål)

Pristipoma nageb: Richardson, 1846 : 227 (one Vachell specimen) (Reeves illustr. No. 244).
Pristipoma hasta: Günther, 1859, **1** : 289 (Reeves and other Chinese material).

Listed as *P. hasta* " China. Rev. G. Vachell " in Harmer's catalogue—destroyed. Günther retained *P. nageb* as a separate species (1859, p. 290), but mentioned no Cambridge material and only tentatively placed Richardson's record in the synonymy. Fowler (1939*a*) considered Richardson's record to refer to *P. argenteus* (Forssk.) and the Reeves illustration is consistent with this.

Family **THERAPONIDAE**

40. ***Therapon jarbua*** (Forsskål)

Therapon servus: Richardson, 1846 : 238 (no Vachell specimens mentioned) (Reeves illustr. No. β44).
Therapon servus: Günther, 1859, **1** : 278 (Reeves and other Chinese specimens).

Listed as *T. servus* " China. Rev. G. Vachell " by Harmer, several specimens—destroyed. Richardson included three other species of *Therapon* (*T. theraps*, *T. oxyrhynchus* and *T. quadrilineatus*), none of which were represented by Vachell material. Identification based on Fowler (1939*b*, p. 204).

Family **SPARIDAE**

41. ***Chrysophrys major*** (Temminck & Schlegel)

Pagrus unicolor: Richardson, 1846 : 242 (Vachell specimen) (Reeves illustr. No. 160).
Pagrus unicolor: Günther, 1859, **1** : 468 (One Hong Kong fish presented by Richardson).

Listed as *P. major* by Harmer " [A specimen from China, Rev. G. Vachell, was lost by evaporation of spirit] " Identification based on Fowler (1940, p. 53).

42. ***Sparus latus*** (Houttuyn)

?Chrysophrys berda: Richardson, 1846 : 240 (no Vachell material) (Reeves illustr. No. 223).
Chrysophrys hasta: Günther, 1859, **1** : 491 (the Reeves type and other Chinese specimens).

Listed as *C. hasta*, " China (? Rev. G. Vachell) " by Harmer—destroyed. Richardson gives nine species of *Chrysophrys*, none of which included Vachell material. He placed *Sparus hasta* Bloch & Schn. in his synonymy of *C. berda*. Identification follows Chu (1931).

Family **MULLIDAE**

43a. ***Upenoides subvittatus*** (Temm. & Schl.)

Upeneus subvittatus: Richardson, 1846 : 219 (one Vachell fish, 4 inches).
Mullus subvittatus: Günther, 1859, **1** : 397 (doubtful species No. 2).

Not listed in Harmer's catalogue. Fowler (1941) listed this Richardson record under *Upeneus subvittatus*.

43b. ***Upenoides subvittatus***(Temm. & Schl.)

Upeneus russelii: Richardson, 1846 : 220 (one injured Vachell specimen) (Reeves illustr. α36).
Upeneus indicus: Günther, 1859, **1** : 406 (two Reeves stuffed specimens, no others).

Not listed by Harmer. Fowler (1941) identified Richardson's record as *Pseudupeneus indicus* (Shaw).

Family SCIAENIDAE

44. ***Otolithes argenteus*** (Cuvier)

Otolithus argenteus: Richardson, 1846 : 225 (one Vachell specimen, 6·55 inches).
Otolithus argenteus: Günther, 1860, **2** : 310 (Reeves and East India Co. specimens).

Not included in Harmer's list. The identifications of the three sciaenids listed here are based on the recent work by Chu, Lo & Wu (1963).

45. ***Collichthys lucidus*** (Richardson)

Sciaena lucida Richardson, 1844 : 87, and 1846 : 224 (see below).
Collichthys lucida: Günther, 1860, **2** : 312 (Reeves and other Chinese specimens).

Listed as *Collichthys lucida* " China. Rev. G. Vachell " in Harmer's catalogue—destroyed. Richardson made no direct reference to Vachell material but states " forms part of all the collections of Chinese fish that we have examined ". Richardson described the species (*Zoology of Sulphur*, p. 87) on material in the British Museum, Hasler Museum and Camb. Phil. Soc. He measured a single specimen, 6·45 inches in length. There are two British Museum fishes labelled as types (BMNH. 1848.3.18.107–8) ; the larger of the two (163 mm. tot. l., 6·4 inches) is most likely the specimen measured by Richardson. There are also two Haslar specimens (BMNH. 1855.9.19.195–7).

46. ***Dendrophysa russelii*** (Cuvier)

Umbrina russelii: Richardson, 1846 : 226 (one Vachell fish) (Reeves illustr. No. β37).
Umbrina russellii: Günther, 1860, **2** : 278 (Malaya and " China Seas? ").

Listed by Harmer as *Umbrina russellii* " ? E. Indies "—destroyed.

Family SILLAGINIDAE

47. ***Sillago japonica*** (Temm. & Schl.)

Sillago japonica: Richardson, 1846 : 223 (Vachell and Reeves specimens) (Reeves illustr. No. β40).
Sillago sihama: Günther, 1860, **2** : 243 (Reeves and China specimens).

Listed as *S. japonica* " China. Rev. G. Vachell " by Harmer, three specimens—destroyed. Günther (1860) referred all his Chinese material to *S. sihama* and not *S. japonica* ; presumably he changed his mind by the time he came to re-identify the Cambridge specimens. Identification based on Chu (1931).

Family EPHIPPIDAE

48. ***Platax orbicularis*** (Forsskål)

Platax teira: Günther, 1860, **2** : 492 (China specimens).

Harmer lists *Platax teira*, 2 specimens " China. Rev. G. Vachell." but, as shown earlier, the actual specimens are the types of *Seserinus vachellii*. Richardson (1846,

p. 245) lists *P. ehrenbergii* Cuvier and *P. vespertilis* Bloch, both of which he identified from Reeves drawings ; in neither case does he mention specimens. Although the present specimens were mislabelled, the name *Platax teira* is included in this list of possible Vachell material.

49. *Drepane punctata* (Linnaeus)

Drepane longimana: Richardson, 1846 : 245 (one Vachell fish) (Reeves illustr. No. 241).
Drepane punctata: Günther, 1860, **2** : 62 (two China specimens).

Not listed by Harmer. Identification follows Fowler (1953, p. 12).

Family SCATOPHAGIDAE

50. *Scatophagus argus* (Linnaeus)

Scatophagus argus: Richardson, 1846 : 245 (two Vachell fishes) (Reeves illustr. No. " 272? ").
Scatophagus argus: Günther, 1860, **2** : 58 (one Reeves and other Chinese specimens).

Listed by Harmer as " ? Fam. ?*Scatophagus argus* (2) ?History "—destroyed. Identification follows Fowler (1953, p. 14).

Family ACANTHURIDAE

51. *Teuthis fuscescens* (Houttuyn)

Amphacanthus margaritiferus: Richardson, 1846 : 243 (one Vachell specimen, 7 inches) (Reeves illustr. No. 259).
Teuthis albopunctata: Günther, 1861, **3** : 318 (Reeves and other Chinese specimens).

Not listed by Harmer. Identification based on Chu (1931).

Family SCORPAENIDAE

52. *Vespicula trachinoides* (Cuvier)

Apistes trachinoides: Richardson, 1846 : 213 (one Vachell fish).
Prosopodasys trachinoides: Günther, 1860, **2** : 139 (one Richardson specimen).

Listed by Harmer as *Prosopodasys trachinoides* " ? East Indies "—destroyed. Richardson (p. 213) also lists the British Museum specimen, collected by Sir Edward Belcher. Identification follows Chu (1931).

53. *Sebastodes vachellii* (Richardson)

**Sebastes vachellii* Richardson, 1846 : 214 (one Vachell specimen, the TYPE) (Reeves illustr. No. 69?).
Sebastes vachellii: Günther, 1860, **2** : 95 (doubtful species No. 1).

Not listed by Harmer ; not amongst type material in British Museum.

Reeves illustration reproduced here (Plate 2, fig. 3). W. L. Chan (*in litt.*) states that the caption to the Reeves illustration, pronounced in Hong Kong as *Sek-gwau-*

kwung (*Shih kow kung* in the " Report "), refers to one of the commonest of Hong Kong inshore fishes, *Sebastiscus marmoratus* (Cuv.), and that the drawing agrees with this. However, Richardson listed *Sebastes marmoratus* (" Report ", p. 215), based on a Bürger specimen in the British Museum, but was not able to identify a Reeves drawing with it. Further, he speaks of the " uncertainty of the drawing " of *S. vachellii*, citing it as " *Icon.* Reeves, 69? ". Since there are two intergrading colour forms of *S. marmoratus* (Matsubara, 1943, p. 256), it is possible that Richardson did not recognize the Reeves drawing as that species.

Neither Matsubara (*loc. cit.*) nor Chu, Tchang & Chen (1963) mention Richardson's *S. vachellii*, and in the absence of the single Vachell specimen we have merely followed the synonymy of Chu (1931), one of the few authors to list this name.

Family SYNANCEJIDAE

54. *Inimicus japonicus* (Cuvier)

**Pelor tigrinum* Richardson, 1846 : 212 (one Vachell specimen, the TYPE) (Reeves illustr. No. β42).
Pelor japonicum: Günther, 1860, **2** : 151 (two Reeves specimens).

Listed as *P. japonicum* " China. Rev. G. Vachell " by Harmer—EXTANT. Reeves illustration reproduced here (Plate 3, fig. 1). See Section 5 (p. 154) for notes on extant specimen.

55. *Minous monodactylus* (Bloch)

Minous woora: Richardson, 1846 : 213 (one Vachell fish).
Minous monodactylus: Günther, 1860, **2** : 148 (Chinese specimens).

Listed as *M. monodactylus*, " = *Apistus minous*, Cuv. (2) China. Rev. G. Vachell." by Harmer—destroyed. Identification follows Chu, Tchang & Chen (1963).

56. *Polycaulus uranoscopus* (Bloch & Schneider)

Synanceia breviceps Richardson, 1844 : 71 (one Reeves and three Vachell fishes).
Aploactis breviceps: Richardson, 1846 : 212 (three Vachell fishes).
Polycaulus elongatus: Günther, 1860, **2** : 175 (one Reeves fish, later cancelled, presumed destroyed).

Listed as " *Polycaulus elongatus* (3) = *Synanceia breviceps*, Richards. China Rev. G. Vachell." by Harmer—destroyed. Identification follows Chu (1931).

Family PLATYCEPHALIDAE

57. *Platycephalus indicus* (Linnaeus)

Platycephalus insidiator: Richardson, 1846 : 216 (one Vachell specimen).
Platycephalus insidiator: Günther, 1860, **2** : 177 (Reeves and other China specimens).

Listed as *P. insidiator* " China. Rev. G. Vachell " by Harmer, three specimens—destroyed. Identification based on Chu (1931).

58. ***Thysanophrys crocodilus*** (Tilesius)

Platycephalus guttatus: Richardson, 1846 : 217 (one Vachell fish).
Platycephalus guttatus: Günther, 1860, **2** : 183 (no specimens—doubtful species).

Not listed by Harmer. Chu, Tchang & Chen (1963) place Richardson's record in *Inegocia guttata* (Cuvier). The synonymy of Chu (1931) is followed here.

Family **POMACENTRIDAE**

59. ***Amphiprion bicinctus*** (Rüppell)

Amphiprion chrysargyrus Richardson, 1846 : 254 (on Reeves drawing only) (Reeves illustr. No. L26).
Amphiprion clarkii: Günther, 1862, **4** : 5 (Reeves and other China material, including one stuffed fish collected by Reeves, the TYPE of *A. chrysargyrus*).

A. chrysogaster " China. Rev. G. Vachell " is listed by Harmer (possibly an error since that is an Indian Ocean species) 2 fishes—destroyed. Richardson mentions no specimens but based the species on a Reeves drawing ; in fact a Reeves fish (stuffed) is present in the British Museum collections. Fowler (1954) placed Richardson's *A. chrysargyrus* in the synonymy of *A. xanthurus* Cuvier, but the pattern of white bands in the Reeves drawing corresponds much more nearly with Fowler's figure 1 for *A. bicinctus.*

Family **LABRIDAE**

60. ***Halichoeres nigrescens*** (Bloch & Schneider)

**Julis exornatus* Richardson, 1846 : 258 (Bankier specimens from Hong Kong, and Vachell and Reeves material—TYPES).
Platyglossus dussumieri: Günther, 1862, **4** : 143 (Reeves and other China specimens, including TYPES of *Julis exornatus*).

Not listed by Harmer. Günther listed China specimens as types of *J. exornatus* (BMNH. 1851.12.27.1634). The Vachell fishes can be considered to have been syntypical material. Two Richardson specimens in British Museum from Hong Kong (BMNH. 1848.3.8.6 and 1868.3.19.833). It is possible that these are Vachell specimens, but there is no evidence to show it. Reeves illustration reproduced here (Plate 3, fig. 4). Identification based on Fowler (1956, p. 230).

Family **GOBIIDAE**

61. ***Glossogobius giuris*** (Ham. Buch.)

Gobius fasciato-punctatus: Richardson, 1846 : 204 (Vachell fish or fishes) (Reeves illustr. No. 146).
Gobius giuris: Günther, 1861, **3** : 21 (Reeves type of *G. fasciato-punctatus* in British Museum and other China specimens).

Not listed by Harmer. Identifications and synonymies for the eleven gobioid species listed here have been based on Koumans (1931, 1953).

62. ***Glossogobius brunneus*** (Tem. & Schl.)

**Gobius platycephalus* Richardson, 1846 : 204 (one Vachell fish, the TYPE, " not in very good condition ") (Reeves illustr. No. L94).
Gobius platycephalus: Günther, 1861, **3** : 5 (doubtful species No. 39, related to *G. brunneus*).

Not listed by Harmer. In the addenda to the " Report " Richardson states (p. 318) that he had just seen the description of *G. brunneus* by Temminck and Schlegel and he considered his *G. platycephalus* probably identical to that species. Vachell fish not amongst types in British Museum. Reeves illustration reproduced here (Plate 3, fig. 3). Fowler (1960) considered *G. brunneus* a synonym of *G. giuris*.

63. ***Cryptocentrus filifer*** (Valenciennes)

Gobius filifer: Richardson, 1846 : 205 (Vachell material).
Gobius knutteli: Günther, 1861, **3** : 73 (Reeves and other China specimens).

Listed as *G. knutteli* " China. Rev. G. Vachell." by Harmer—destroyed. A second Vachell specimen listed by Harmer as " [Origl. label = *G. filifer*] (probably the specimen alluded to by Richardson, in Brit. Assn. Report, 1845, p. 205) "—destroyed also.

64. ***Rhinogobius margariturus*** (Richardson)

**Gobius margariturus* Richardson, 1846 : 205 (one, perhaps more, Vachell specimens—TYPE) (no Reeves illustr.).
Gobius margariturus: Günther, 1861, **3** : 47 (on Richardson, no specimens listed).

As *G. margariturus* " China. Rev. G. Vachell " in Harmer's list—destroyed. Vachell specimen not amongst types in British Museum. Fowler (1960) placed this species in *Ctenogobius* and commented " A rare species, apparently not seen since described in 1846."

65. ***Drombus ripilepis*** (Richardson)

**Gobius ripilepis* Richardson, 1846 : 205 (one Vachell fish, the TYPE, 3½ inches) (no Reeves illustr.).
Gobius ripilepis: Günther, 1861, **3** : 5 (doubtful species No. 28, apparently allied to *G. kokius* ").

Not included in Harmer's list. Placed in *Ctenogobius* by Fowler (1960).

66. ***Acanthogobius stigmothonus*** (Richardson)

**Gobius stigmothonus* Richardson, 1844 : 147, and 1846 : 205 (two Vachell fishes of 5 or 6 inches —the TYPES) (no Reeves illustr.).
Gobius stigmothonus: Günther, 1861, **3** : 76 (no specimens).

Listed as *G. stigmothonus* (3 fishes) " China. Rev. G. Vachell " by Harmer—destroyed. The species was described by Richardson in the *Zoology of the Sulphur* (1844, p. 147) and was based on " . . . several specimens . . . brought from Canton by the Rev. George Vachell ". The Vachell specimens are not amongst the types in the British Museum.

67. *Apocryptes serperaster* (Richardson)

**Apocryptes serperaster* Richardson, 1846 : 206 (two Vachell specimens, 6 inches in length—the Types) (Reeves illustr. No. β55).
Apocryptes serperaster: Günther, 1861, **3** : 82 (Reeves and other China specimens).

Listed by Harmer as *A. serperaster* " ? China Rev. G. Vachell [labelled " Reeves "]" —destroyed. The words " Rev. G. Vachell " are crossed out, perhaps when the reference to Reeves was added. A Reeves specimen of 6 inches is in the British Museum, now labelled as a type, BMNH. 1965.8.12.51. It has a metal tag tied to the jaw " 19.2.3.". Reeves illustration reproduced here (Plate 3, fig. 2).

Family PERIOPHTHALMIDAE

68a. *Boleophthalmus pectinirostris* (Linnaeus)

Boleophthalmus boddaerti: Richardson, 1846 : 208 (Vachell material) (Reeves illustr. No. β38).
Boleophthalmus boddaerti: Günther, 1861, **3** : 102 (Indian Ocean specimens only).

Not included in Harmer's list. Fowler (1962) distinguished *B. boddaerti* (Pallas) from *B. pectinirostris* mainly on the presence in the former of dark transverse badns on the body. The Reeves drawing does not show these bands.

68b. *Boleophthalmus pectinirostris* (Linnaeus)

Boleophthalmus pectinirostris: Richardson, 1846 : 208 (one Vachell fish, 2·80 inches).
Boleophthalmus pectinirostris: Günther, 1861, **3** : 102 (Reeves specimen).

Not included in Harmer's list. Unregistered Reeves specimen in British Museum of 132 mm. tot. l., and an unregistered Haslar specimen of 106·5 mm. tot. l., labelled merely " 158 ". Both are too large to have been the Vachell fish.

69a. *Scartelaos histophorus* (Valenciennes)

Boleophthalmus aucupatorius Richardson, 1844 : 148, and 1846 : 208 (Vachell material).
Boleophthalmus viridis: Günther, 1861, **3** : 104 (" b,c. Half-grown. China. Presented by Sir J. Richardson—Types of *B. aucupatorius*.").

Not included in Harmer's list. Described by Richardson in the *Zoology of the Sulphur* (1844, p. 148), based on fishes collected by Sir Everard Home, John Reeves and the Rev. George Vachell. Two Chinese specimens in the British Museum (BMNH. 1965.8.12.52–3) presented by Richardson ; the larger of the two (2·65 inches total length) is undoubtedly Richardson's measured and figured specimen. There is no indication, however, that these are Vachell specimens.

69b. *Scartelaos histophorus* (Valenciennes)

Boleophthalmus campylostomus Richardson, 1846 : 209 (no specimens, see below) (Reeves illustr. No. β52).
Boleophthalmus campylostomus: Günther, 1861, **3** : 101 (doubtful species No. 2).

Listed by Harmer as the type of *B. campylostomus,* ' China. Rev. G. Vachell "—

EXTANT. Richardson, however, based his description solely on the Reeves drawing, stating " Of this fish we have seen no specimen." This Cambridge specimen was presented to the British Museum (BMNH. 1917.7.14.89) and has hitherto been labelled wrongly as a type. See Section 5 (p. 155) for description and notes.

Family **GOBIOIDIDAE**

70a. ***Taenioides anguillaris*** (Linnaeus)

Amblyopus rugosus: Richardson, 1846 : 207 (Vachell material) (Reeves illustr. No. β7).
Amblyopus rugosus: Günther, 1861, **3** : 133 (doubtful species No. 4—" Typical specimens in Cambridge Museum ").

Not included in Harmer's list. The synonymy of Fowler (1962) is followed for the two Richardson *Amblyopus* records.

70b. ***Taenioides anguillaris*** (Linnaeus)

Amblyopus anguillaris: Richardson, 1846 : 207 (two Vachell fishes, 4·80 inches).
Amblyopus hermannianus: Günther, 1861, **3** : 135 (one China specimen).

Listed as " *Amblyopus hermannianus* = ' *A. anguillaris* '. China. Rev. G. Vachell " by Harmer—destroyed.

Family **TRYPAUCHENIDAE**

71. ***Trypauchen vagina*** (Bloch & Schneider)

Trypauchen vagina: Richardson, 1846 : 206 (Vachell material) (Reeves illustr. No. β57).
Trypauchen vagina: Günther, 1861, **3** : 137 (China specimens).

Listed by Harmer as *T. vagina*, three specimens " ? Histy."—destroyed. Identification follows Fowler (1962).

Family **CALLIONYMIDAE**

72. ***Callionymus hindsii*** (Richardson)

Callionymus hindsii: Richardson, 1846 : 210 (one Vachell fish).
Callionymus hindsii: Günther, 1861, **3** : 146 (four Belcher specimens—the types of *C. hindsii*).

Listed as *C. hindsii* " China. Rev. G. Vachell " by Harmer—destroyed. Identification based on Fowler (1959).

73. ***Callionymus japonicus*** (Houttuyn)

Callionymus reevesii Richardson, 1844 : 60 (one Belcher fish) and 1846 : 210 (two female fishes, Vachell) (Reeves illustr. No. 180—female according to Richardson).
Callionymus longecaudatus: Günther, 1861, **3** : 148 (China specimens).

Harmer listed two specimens of *C. longecaudatus* = " *C. reevesii* ♀ ' Zool. of Sulph.' by Richards."—destroyed. These are not the types, since Richardson described this species (*Voyage of the Sulphur*, 1844, p. 60) on a single specimen collected by Sir Edward Belcher, which he considered a male. Günther (1861, p. 145) tentatively placed Richardson's female (i.e. Vachell) *C. reevesii* in the synonymy of *C. curvicornis* Valenciennes, and placed the male in *C. longecaudatus* Temm. & Schl.; but in a note on the latter species (p. 148) he cites Bleeker's opinion that all Chinese specimens should be referred to *C. reevesii*. Fowler (1959) considered *C. reevesii* a junior synonym of *C. japonicus*, although he placed Richardson's *Voyage of the Sulphur* figure in *C. curvicornis* (referring to it as a female).

Family **MUGILOIDIDAE**

74. ***Parapercis pulchella*** (Temm. & Schl.)

Percis pulchella: Richardson, 1846, 211 (one Vachell fish).
Percis pulchella: Günther, 1860, **2** : 240 (Japan and Haslar specimens).

Not listed by Harmer. Richardson suspected that *P. pulchella* was merely a variety of *P. nebulosa* Cuvier. Identification follows synonymy of Chu (1931).

Family **URANOSCOPIDAE**

75. ***Uranoscopus japonicus*** (Houttuyn)

Uranoscopus asper: Richardson, 1846 : 211 (one Vachell fish) (Reeves illustr. Nos. 162 and 166).
Uranoscopus asper: Günther, 1860, **2** : 228 (Japanese specimens).

Listed as *U. asper* " China. Rev. G. Vachell " by Harmer—destroyed. Identification based on Chu, Tchang & Chen (1963).

Family **TRIACANTHIDAE**

76. ***Triacanthus biaculeatus*** (Bloch)

Triacanthus biaculeatus: Richardson, 1846 : 202 (no Vachell material) (Reeves illustr. No. *a*24).
Triacanthus brevirostris: Günther, 1870, **8** : 209 (Reeves and other China specimens).

Listed as *T. brevirostris* " China. Rev. G. Vachell " by Harmer, 2 fishes—EXTANT. These specimens may have been overlooked by Richardson. The latter evidently misidentified the Reeves drawing, which from its coloration is definitely *T. brevirostris*. For notes and description of the two extant specimens, see Section 5 (p. 156).

Family **BALISTIDAE**

77. ***Abalistes stellatus*** (Bloch & Schneider)

**Balistes vachellii* Richardson, 1844 : 129, and 1846 : 201 (one Vachell specimen—the TYPE).
Balistes stellatus: Günther, 1870, **8** : 212 (one China specimen, very young, Belcher).

Included in Harmer's list as *B. stellatus* " No histy."—destroyed. Richardson based his description of this species (*Zoology of the Sulphur*, p. 129) on a single Vachell specimen of " 3·75 inches " preserved in spirit. Identification follows synonymy of Chu (1931).

78. *Alutera scripta* (Osbeck)

Aleuteres laevis: Richardson, 1846 : 202 (no specimens mentioned).
Monacanthus scriptus: Günther, 1870, **8** : 252 (no China specimens).

Listed as *M. scriptus* " China. Rev. G. Vachell " by Harmer, 2 fishes—destroyed. These were either missed by Richardson or were not true Vachell fishes. Identification based on Chu (1931), but generic allocation follows Schultz (1966).

Family TETRAODONTIDAE

79. *Fugu* (*Torafugu*) *ocellatus* (Linnaeus)

Tetrodon ocellatus: Richardson, 1846 : 199 (no Vachell material mentioned) (Reeves illustr. Nos. 96 *O* and 271).
Tetrodon ocellatus: Günther, 1870, **8** : 279 (Reeves and other China specimens).

Listed by Harmer as *T. ocellatus* two specimens " China. Rev. G. Vachell "—destroyed. Harmer also listed an exhibited specimen F4227, (EXTANT, 102 mm S.L., 127 mm. tot. l.), but it seems doubtful that this is a Vachell specimen since Richardson mentions spirit specimens only in the " British Museum and Chinese collection at Hyde Park ". See Section 5 (p. 157) for notes on this specimen.

Family ECHENEIDAE

80. *Echeneis naucrates* (Linnaeus)

Echeneis naucrates: Richardson, 1846 : 203 (no Vachell material mentioned) (Reeves illustr. No. 97h).
Echeneis naucrates: Günther, 1860, **2** : 384 (Reeves and Richardson specimens).

Listed as *E. naucrates* in the Exhibited Catalogue No. F.2917 " Specimen in spirit. China Seas. Cambridge Philosl. Society's Colln." This specimen is still extant—see notes on p. 157. (There is another extant specimen listed by Harmer in the non-exhibited catalogue as " (juv.) ? History.) "

5. EXTANT VACHELL SPECIMENS

Apart from one, the few remaining extant specimens from the Vachell collection are in the University Museum of Zoology in Cambridge. The exception is a single fish sent from Cambridge to the British Museum (Natural History), *Boleophthalmus campylostomus*, which is labelled " Vachell ", but in this case Richardson clearly stated that he had seen no specimens of that species. The extant specimens in Cambridge mostly bear recent labels indicating their origins. Authority for this presumably derives from Harmer's catalogue, unless contemporary labels once existed and were subsequently destroyed ; Harmer only once mentions such an original label, i.e. for *Cryptocentrus filifer* (p. 143). In only one instance is there a label tied to the fish (*Coilia playfairii*), but even then the label merely states the name of the fish and not its origin. In the case of the Exhibited Series at Cambridge, the name of the species, the place of capture and the collector are inscribed, either on a porcelain plate supporting the specimen (e.g. for *Anguilla clathrata* and *Caranx armatus*), or on a small " perspex " plate glued inside a modern " perspex " box. In a few cases, the size of the specimen agrees with that given by Richardson in his description and the fish can be certainly identified as one of the Vachell collection. But in most cases this is not possible; either Richardson gives no lengths, or else the specimen has been listed by Harmer as " Vachell " but is not mentioned by Richardson. Thus there can be no certainty of the number of extant Vachell specimens.

In the following descriptions and notes we have included eleven species (fifteen specimens) which may be Vachell material :

No. 5. " *Coilia playfairii* " (=*Coilia playfairii*)
No. 7. " *Anguilla clathrata* " (=*Anguilla japonica*) HOLOTYPE
No. 18. " *Holocentrum albo-rubrum* " (=*Holocentrus ruber*)
No. 23. " *Trichiurus intermedius* " (=*Lepturacanthus savala*)
No. 25. " *Seserinus vachellii* " (=*Parastromateus niger*) SYNTYPES
No. 30. " *Caranx ciliaris* " (=*Citula armata*)
No. 54. " *Pelor tigrinum* " (=*Inimicus japonicus*) HOLOTYPE
No. 69*b*. " *Boleophthalmus campylostomus* " (=*Scartelaos histophorus*)
No. 76. " *Triacanthus biaculeatus* " (=*Triacanthus biaculeatus*)
No. 79. " *Tetrodon ocellatus* " (=*Fugu* (*Torafugu*) *ocellatus*)
No. 80. " *Echeneis naucrates* " (=*Echeneis naucrates*)

The following abbreviations have been used in the descriptions of specimens :

D	dorsal fin rays	S.L.	standard length
P	pectoral fin rays	tot. l.	total length
V	pelvic fin rays	BMNH.	British Museum (Natural History)
A	anal fin rays		
g.r.	gillrakers	UMZC.	University Museum of Zoology, Cambridge (non-exhibited catalogue, roman numbers; exhibited catalogue, F numbers).
Br.St.	branchiostegal rays		

Unless stated otherwise, measurements were made in the following manner :

body depth: usually under dorsal origin, otherwise at deepest point.
head length: from premaxillary symphysis to edge of operculum, the longest measurement (i.e. not always horizontal).
gape: from dentary symphysis to angle of jaw.
upper jaw: from snout tip to posterior tip of maxilla.

In the fin ray formulae, spines are indicated in roman capitals, simple rays in lower case roman numerals, and branched rays in arabic numerals. Scutes are expressed as pre-pelvic and post-pelvic, with the scute lying between the pelvic fins counted as the first post-pelvic scute.

5. " *Coilia playfairii* "

= *Coilia playfairii* (McClelland, 1844)

A single fish, 268·5 mm. S.L. (290 mm. tot. l., caudal tip broken), scales mostly shed, otherwise in fair condition, label tied to caudal peduncle " *Coilia mystus* Engrauli[dae] ", modern label in bottle giving locality as " Canton " but with no mention of Vachell, UMZC. VII, 404 (catalogued as " Fishes from China ". Canton).

Description. Br.St. 12, D I + iii 11, P 7 free + 11 (left) and 7 free + 12 (right), V i 6, A ii 84, g.r. 28, scutes 15 + 26.

In percentages of standard length : body depth 17·9, head length 16·8 ; snout length 3·7, eye diameter 3·4, length of upper jaw 22·0, length of lower jaw 11·9 ; pectoral fin length 37·9 (filaments) and 10·9 (longest branched ray), pelvic fin length 7·1, length of anal base 55·4 ; pre-dorsal distance 29·3, pre-pelvic distance 26·2, pre-anal distance 41·3.

Head a little broader than body. Body compressed, its width 3 times in its depth, belly sharply keeled, with scutes beginning on isthmus ; ascending arms of post-pelvic scutes alternately long and short. Maxilla reaching beyond base of first pectoral ray by about 1 eye diameter, toothed along entire lower border ; two supra-maxillae present, the second expanded posteriorly and curved downwards at its tip, the first longer than deep. Lower jaw, with prominent knob at symphysis, rising posteriorly to form high coronoid process.

Gillrakers moderately slender, about 4/5 eye diameter and 1½ times length of corresponding gill filaments ; gillraker serrae of even length except those near the tips of the rakers ; no gillrakers on the posterior face of the 3rd epibranchial. Muscular portion of isthmus reaching forward to the hind border of the branchiostegal membrane.

Dorsal preceded by small spine ; dorsal origin slightly behind pelvic origin. Pectoral with seven long filaments, separate throughout their length, tip of longest filament reaching to base of 15th anal branched ray. Pelvic base nearer to base of 1st pectoral ray than to anal origin by 1½ eye diameters. Posterior part of body not tapering to a point, 6·5 mm. deep at caudal base. Anal origin behind vertical from last dorsal ray by 3 eye diameters.

Colour: upper ¼ light brown, rest of flanks silvery except for narrow brown strip above base of anal finrays in posterior half of fin. Fins hyaline.

Note: Richardson stated that specimens of *C. playfairii* existed in all the Chinese collections which he examined, but he does not specifically mention any Vachell material. Further notes on this species are given by Whitehead (1966).

7. " *Anguilla clathrata* "

= *Anguilla japonica* Temminck & Schlegel, 1846

A single fish, 228 mm. S.L. (232 mm. tot. l.) in good condition, mounted for exhibition with printed label " *Anguilla vulgaris* China. Rev. G. Vachell ", UMZC.

F.2002. Originally catalogued as VIII 28 *Anguilla vulgaris*. China. Rev. G. Vachell, and subsequently transferred to the exhibited series. HOLOTYPE of *Anguilla clathrata* Richardson.

DESCRIPTION. Br.St. (not recorded), D 225, P i 16, A 222 (counts made from radiograph of holotype).

In percentages of standard length : body depth 4·2, head length 10·5 ; snout length 1·8, eye diameter 0·95, interorbital width 1·2, gape 2·58 ; pectoral fin length 3·4 ; pre-pectoral distance 10·6, pre-dorsal distance 29·4, pre-anal distance 38·2 ; distance between verticals from dorsal and anal origins 9·6.

Pre-anal length without head 27·3% of total length. Distance between verticals from dorsal and anal origins 9·5% in total length (i.e. slightly less than head length). Gape 24·7% in head length, eye diameter 9·0% in head length.

Lower jaw projecting slightly. Maxillary tooth bands with two rows of conical teeth with a longitudinal groove between them. Average breadth of pre-maxillary-vomerine tooth band only slightly greater than the width of the maxillary bands ; the former with 2–3 longitudinal rows of teeth.

Vertebrae 115, of which 44 are prehaemal (from radiograph).

Colour: back and flanks light brown, becoming almost cream on the belly ; no evidence that the flanks were ever marbled or mottled. Fins hyaline, but a distinct dark brown margin round the posterior 12 mm. of the tail region.

Note: In his revision of the genus *Anguilla*, Ege (1939) omitted a number of names from his synonymies, some of which were discussed later in the text, but not the name *clathrata*. Günther's apparent neglect of the type of *Anguilla clathrata* has probably accounted for the fact that it has been generally overlooked. It is listed as distinct from *A. japonica* by Chu (1931), but this author did not examine the type.

Following the keys and descriptions of Ege (*loc. cit.*) the present specimen is undoubtedly *Anguilla japonica*. The tooth bands in the upper jaw resemble those shown for a typical specimen by Ege (*loc. cit.*, Pl. 23, fig. 5). The positions of the dorsal and anal fins agree with the formulae given by Ege, as also the relation between the gape of the mouth and the length of the head. Of great importance is the dark margin round the tail, a character stated by Ege to occur only in *A. japonica*. On geographical grounds, the only other species likely to be found in that area is the mottled eel *Anguilla marmorata* Quoy & Gaimard. In that species, however, the distance between the verticals from dorsal and anal origins much exceeds the length of the head. Also, Ege gives the vertebral numbers for *A. marmorata* as 100–110 (115 in the type of *Anguilla clathrata*). *Anguilla borneensis* Popta, another possibility, also has a much lower vertebral count (103–108).

The name *Anguilla japonica* Temm. & Schl. has been very widely used for the Japanese freshwater eel for over a century. Unfortunately, the name *Anguilla clathrata* pre-dates it by two years, and is not a *nomen oblitum* since it was used as a senior synonym by Chu (1931). It would, however, be greatly in the interests of stability if the name *japonica* were retained, and an application to the International Commission has been made (Whitehead, 1966*a*).

18. " ***Holocentrum albo-rubrum*** "

= ***Holocentrus ruber*** (Forsskål, 1775)

Two fishes, 131·2 and 137·7 mm. S.L. (175 and 166 mm. tot. l., estimated for larger fish since caudal tips damaged), in fair condition, modern label " *Holocentrum rubrum* China Rev. G. Vachell " (repeat of entry in catalogue), UMZC. I, 35.

DESCRIPTION. (figures for the larger fish cited first) Br.St. 7 and 7, D XI 14 and XI 14, P 2 + i 12 and 2 + i 12, V I 7 and I 7, A IV 9 and IV 9, g.r. 6 + 10 and 8 + 10, scales 36 and 36, $2\frac{1}{2}/7$ and $2\frac{1}{2}/7$, 6 predorsal, 5 series on cheek, 1 series on operculum.

In percentages of standard length : body depth 38·0 and 39·6, head length (excluding opercular spine) 32·8 and 33·2 (including spine, 36·4 and 37·4) ; snout length 8·3 and 7·9, eye diameter 11·7 and 12·3, interorbital width (above eye centre) 8·0 and 9·4, upper jaw length 14·1 and 14·5 ; caudal peduncle, length 13·4 and 13·3, depth 9·7 and 10·2—length depth ratio 1·38 and 1·71.

Body deep, compressed, its width 1·45 times in its depth. Upper profile descending rather abruptly from occiput to snout tip. Jaws equal, maxilla almost reaching to vertical from eye centre, expanded distal portion $2\frac{3}{4}$ in eye. Nostrils two, close together and lying immediately in front of the eye ; bony ridges in front of nostril ending in blunt spine over pre-maxilla. Lower border of preorbital with small spines, anterior one largest ; upper pre-orbital ridge with triangular spine below anterior eye border, directed laterally. Infra-orbital and post-orbital finely denticulated. Two flat spines at upper angle of operculum, upper one longest and reaching back beyond gill opening ; posterior part of operculum with parallel ridges ending in sharp serrae along posterior border. Pre-opercular spine stout, about 7/8 eye diameter ; outer borders of pre-operculum and suboperculum with fine serrae. Fronto-parietal region with about 8 parallel ridges, one on each side extending forward between the orbits ; a patch of fine denticulations above posterior half of eye.

Dorsal origin above tip of lower opercular spine ; spines stout, the 4th longest, space between the 1st and 2nd narrow ; membranes between spines deeply incised. Anal with 3rd spine longest, about twice eye diameter, 1st spine minute. Pelvic origin below vertical from between 2nd and 3rd dorsal spines ; pelvic spine about $1\frac{3}{4}$ times eye diameter.

Colour: Light brown, with the appearance of about seven longitudinal light fawn lines down the flanks (along scale rows). Smaller fish with dark markings at the base of the upper opercular spine, in the membrane between the first two dorsal spines, at the base of the soft part of the dorsal, at the tips of the pelvic soft rays, in the membrane between the 3rd anal spine and the first of the branched anal rays, and along the outer caudal rays. Richardson states " There is none of the yellow colour on the fins which the preceding species [i.e. *H. spinosissimus*] shows ".

Note: these two specimens agree well with the diagnosis and description of Yu (1963), and it must be presumed that the colours were sufficiently well retained when Richardson examined them for him to distinguish these fishes from the closely related

H. spinosissimus Temm. & Schl., of which he had a single specimen (Reeves). Yu (*loc. cit.*) records *H. ruber* as the commonest species of *Holocentrus* in the Taiwan region.

23. " *Trichiurus intermedius* "

= *Lepturacanthus savala* (Cuvier, 1829)

A single fish, 372 mm. S.L. (376 mm. tot. l.), in good condition, mounted for exhibition with printed label " *Trichiurus muticus* Hair Tail China Rev. G. Vachell ", UMZC. F.2685.

DESCRIPTION. Br.St. 6, D iv 111, P i 10, V (absent), A I 82, g.r. 5 + 6–7.

In percentages of standard length : body depth 5·4, head length 11·5 ; snout length 4·36, eye diameter 1·67, upper jaw length 5·0, lower jaw length 7·37 ; pectoral length 4·31 ; pre-dorsal distance 8·4, pre-anal distance 29·5.

Body elongate, tapering, its depth 18·7 times in total length. Head 8·8 times in total length. Lower jaw strongly projecting, with prominent mental lobe. Frontal ridges converging posteriorly to form fairly prominent sagittal crest at nape, the ridge not continued forward onto the ethmo-frontal region. Lower margin of suboperculum slightly concave. Teeth in both jaws caniniform, fang-like anteriorly in the upper jaw. Eye 6·9 times in head (14·5% of head length).

Pectoral fins short, pelvic fins absent. First four dorsal rays weakly spinous, the last about equal in length to the first soft ray. First spinous anal ray apparently absent, second ray enlarged, spinous, 3·1 mm. in length (½ eye diameter) ; anal rays breaking through skin as pungent spinules. No caudal.

Lateral line dipping down sharply behind the pectoral fin base, and thereafter running along the lower ⅓ of flank.

Colour: very pale brown, with a white midlateral line ; fins colourless.

Note: the large post-anal scute (i.e. anal spine I), the presence of pungent anal spinules and the small eye, were used by Tucker (1956) to distinguish *Lepturacanthus* from *Trichiurus*. The present specimen agrees well with Tucker's diagnosis of this monotypic genus.

Harmer listed this fish as *Trichiurus muticus*, a species which Richardson (1846, p. 268) placed in the synonymy of " *Trichiurus lepturus, japonicus* Temm. & Schl.". [Tucker (*loc. cit.*) regarded *T. muticus* Gray as a member of *Eupleurogrammus* Gill, but considered *T. lepturus* Linn. as a true *Trichiurus*]. It is difficult to know how the present specimen came to be labelled *T. muticus* since Richardson does not mention Vachell specimens under any of the three species of *Trichiurus* listed (*T. armatus* Gray, 1831, in the synonymy of which he placed *T. savala* Cuvier ; *T. lepturus* ; and *T. intermedius*). A Reeves illustration exists only for the first of these species. It must be presumed that Richardson either overlooked this Cambridge specimen or that he failed to mention it under *Trichiurus armatus*, only listing the British Museum specimen.

25. " *Seserinus vachellii* "

= *Parastromateus niger* (Bloch, 1795)

Two fishes, 56·6 and 74·7 mm. S.L. (66·8 and 91·1 mm. tot. l.), caudal tips slightly damaged, otherwise in fair condition, modern label in jar " *Platax teira* China Rev. G. Vachell ", UMZC. II, 492 (repeat of entry in catalogue). SYNTYPES of *Seserinus vachellii* Richardson.

DESCRIPTION. (based on the larger of the two specimens, 74·7 mm. S.L.) D 5 rudimentary + I 41, P i 22, V i 5, A 2 rudimentary + I 37, g.r. 6 + 15.

In percentages of standard length : body depth 65·5, head length 31·5 ; snout length 9·4, eye diameter 9·1 ; pectoral fin length 23·0, pelvic fin length 13·5, non-rudimentary dorsal spine 14·2, longest branched dorsal ray 41·2, non-rudimentary anal spine 11·1 ; length of dorsal base 64·0, length of anal base 57·4 ; pre-dorsal distance 47·4, pre-pelvic distance 25·8, pre-anal distance 50·9.

Body strongly compressed, rhombic, dorsal and ventral profile angular. Head with its nuchal contour keeled. A single series of small conical teeth in each jaw. Adipose eyelid barely developed. Mouth a little oblique, maxilla reaching to anterior border of eye. Operculum with faint radial striae.

Dorsal preceded by an antrorse spine, followed by five small retrorse spines and a large spine (about ½ head length) ; 5th branched ray longest, much greater than head length, the rays decreasing in length thereafter. Two rudimentary anal spines, embedded in the skin ; first non-rudimentary anal spine a little larger than eye diameter. Pelvic base below vertical from posterior border of eye.

Caudal peduncle narrow, its depth less than eye diameter. Caudal deeply forked.

Minute cycloid scales present on body. Lateral line scales becoming scuted in posterior ¼ of body, the scutes shield-shaped with a single point.

Colour: flanks light brown, belly lighter, becoming white. Fins hyaline, but dark brown markings on anterior part of dorsal and anal and on upper surface of pelvic fins.

Note: Harmer did not list any specimens under Richardson's name *Seserinus vachellii*. On the other hand, he listed the present specimens as " *Platax teira* ". Even a cursory glance at the specimens in the bottle shows that they are not *Platax* (chiefly the lack of filamentous rays), which suggests that the identification was not made by Günther but was perhaps the result of a curatorial error. The larger syntype tallies with the size given by Richardson.

The name *Formio* was proposed by McCulloch (1929) as a replacement name for *Apolectis* Cuvier, 1832, which was preoccupied by *Apolectis* Bennett, 1831. De Beaufort & Chapman (1951, p. 458) resurrected the name *Parastromateus* Bleeker, 1865 for this genus, and after some hesitation placed this monotypic genus amongst the carangids. McCulloch (*loc. cit.*) had proposed a separate family, the Formiidae, and it is significant that Suzuki (1962), in a comprehensive revision of the Japanese members of the family Carangidae, did not include the present species. We have here followed McCulloch.

The Vachell specimens agree well with the description of the species by De Beaufort & Chapman except in one respect. The 5th branched dorsal ray is over four times as long as eye diameter ; their statement " which is as long as eye " seems to be an error.

30. " *Caranx ciliaris* "

= *Citula armata* (Forsskål, 1775)

A single fish, 88 mm. S.L. (111 mm. tot. l.), mounted for exhibition in glass jar and labelled " *Caranx armatus* " but with no indication of the place of capture or donor, UMZC. F.2755 (catalogued as China. Cambridge Philosoph. Society's Collection).

Both Richardson (1846, p. 276) and Harmer list a Cambridge Philosophical Society specimen but do not state if it was a Vachell fish, nor do they give any indication of the size of the specimen. This fish must be considered as only doubtfully part of the Vachell collection.

For the identification of this specimen we have followed Suzuki (1962).

54. " *Pelor tigrinum* "

= *Inimicus japonicus* (Cuvier, 1829)

A single fish, 191 mm. S.L. (242 mm. tot. l.), in good condition, modern label only " *Pelor japonicum* China Rev. G. Vachell ", UMZC. II, 151 (repeat of entry in catalogue). HOLOTYPE of *Pelor tigrinum* Richardson.

DESCRIPTION. D XVII 7, P 12, V I 5, A II 9, g.r. 2 + 6, pores in lateral line 16.

In percentages of standard length : body depth 36·1, body width 26·2, head length 33·0, head width 35·0 ; snout length 14·3, eye diameter 4·6, interorbital width (above eye centre) 10·7, upper jaw length 17·7, post-orbital distance 13·9 ; pre-dorsal distance 23·8, pre-pelvic distance 25·1, pre-anal distance 60·7 ; depth of caudal peduncle 10·5.

Body a little deeper than wide, head about as wide as deep. Snout length equal to post-orbital distance ; posterior half of snout without narrow longitudinal keel. Mouth moderate, oblique, maxilla reaching to vertical from anterior eye border. Lower jaw projecting when mouth closed, symphysial knob evident ; teeth villiform, in a moderate band in each jaw and on vomer. Orbits well raised, with deep interorbital cavity and transverse ridge linking orbits posteriorly ; deep rectangular depression across occiput ; parietal ridges high, bluntly pointed. Operculum with two ridges, the upper largest and terminating in a blunt spine. Pre-operculum with two spines.

Dorsal origin more than one eye diameter behind orbits ; first three dorsal spines separated from remainder of fin by deep excavation in fin membrane ; longest dorsal spine (7th) 19·2% of S.L., penultimate spine 17·8%, last spine 18·3%, longest soft dorsal ray (3rd) 20·9%. Pelvic about as long as head, entirely adnate, tip of last ray reaching vent. Pectoral equal to head length, its origin below base of 3rd dorsal spine, its tip reaching to vertical from 13th dorsal spine ; two detached rays present. Head, body, dorsal and pectoral covered with small dermal tubercles, and small dermal flaps present posteriorly at tips of dorsal spines.

Colour: most of body and head white except (apparently) parts which have been less exposed to the light, i.e. where right flank is covered by the pectoral and where the dorsal is folded over part of the left flank. In these areas there is evidence of brown mottling, but no overall colour pattern can be distinguished now.

Note: Richardson (1846, p. 212) listed five species of *Pelor: P. japonicum, P. aurantiacum, P. tigrinum, P. cuvieri* and *P. sinense.* Matsubara (1943), whose work has been followed in identifying the present specimen, considered the first three of these nominal species as synonyms.

69b. " **Boleophthalmus campylostomus** "

= **Scartelaos histophorus** (Valenciennes, 1837)

One fish, 70·5 mm. S.L., caudal tip broken, otherwise in good condition, jar labelled " *Boleophthalmus campylostomus* (TYPE) China. Vachell ", formerly in Cambridge, now in the British Museum (Natural History), BMNH. 1917.7.14.89 (catalogued by Harmer as " *Boleophthalmus campylostomus* Richards. TYPE China. Rev. G. Vachell").

DESCRIPTION. D_1 v, D_2 i 26, P 19, V i 5, A i 27

In percentages of standard length : body depth 14·2, body width 9·4, head length 24·5, head width 13·5 ; snout length 4·7, eye diameter 4·25, length of upper jaw 9·5, length of lower jaw 8·8 ; pectoral fin length 12·5, pelvic fin length 11·1, length of 1st dorsal base 5·5, height of 1st dorsal fin 25·0, height of 2nd dorsal fin 5·4 ; pre-1st dorsal distance 36·2, pre-2nd dorsal distance 53·4, pre-anal distance 54·8.

Body moderately elongate, subcylindrical anteriorly, a little compressed posteriorly, its width 1·5 times in its depth. Head a little depressed, its width twice in its length. Snout blunt, a little greater than eye diameter. Eyes close together, lower eyelid well developed. Upper jaw prominent, tip of maxilla almost reaching to vertical from posterior border of eye ; a single series of teeth present in each jaw ; upper jaw with 7–8 curved caninoid teeth with bluntly pointed tips, and a number of smaller and more closely-set teeth, almost concealed, lying nearer to angle of jaw ; lower jaw with a well-developed symphysis bearing a large canine on each side, and about 8 caninoid teeth along jaw with blunt tips (not obliquely truncate), followed by a short series of closely-set smaller caninoid teeth partly concealed. A series of 4 barbels along posterior half of lower jaw ramus, and a single larger mental barbel. Gill openings narrow, oblique, extending from middle of pectoral base to just above pelvic base.

First dorsal fin elongate, a little longer than head length, the 3rd ray the longest. Second dorsal fin low (less than half body depth), last ray not (?now) connected with caudal fin. Pectoral fin rounded, with fleshy base, its tip reaching to just beyond vertical from base of last ray in first dorsal fin. Pelvic fins united, joined to body along almost half their length, tips reaching to vertical from origin of 1st dorsal fin. Anal fin long and low, its origin below 2nd branched ray of 2nd dorsal fin, not (?now) joined to caudal fin posteriorly. Caudal fin damaged.

Head and anterior parts of body covered with warty skin. Scales present from halfway along anal fin to base of caudal fin, minute, partly embedded.

Colour: very pale fawn grading to a cream colour on the flanks and belly ; no sign of spots on the body. Fins white.

Note: This specimen has hitherto been labelled *Boleophthalmus campylostomus*, but re-examination shows that small barbels are present under the lower jaw, a character diagnostic of the monotypic genus *Scartelaos* Swainson. Also, the lower jaw teeth are blunt but are not obliquely truncate, as they are in *Boleophthalmus*. The barbels in the present specimen are not as numerous as shown in the figure given by Koumans (1953, figure 65), or as in the Richardson type of *B. aucupatorius* (=*Scartelaos histophorus*), and this may account for the misidentification of the specimen.

It is noteworthy that this is the only occasion when Harmer records a Vachell fish as a type in his catalogue. This may have been the reason why this fish alone was transferred to the British Museum (in 1917). In fact, the specimen is not a type since Richardson described the species solely on the basis of a Reeves illustration (No. *β*52) and expressly states that he had seen no specimens. It is curious that Harmer lists it as a Vachell fish, but this may be one more case when Richardson overlooked material in Cambridge. Günther (1868, p. 101) considered the species " doubtful ", but presumably it was he who identified the specimen later during one of his visits to Cambridge.

The species has long been known as *Scartelaos viridis* (Ham. Buch., 1822), but Whitley (1929) and Fowler (1962) have pointed to the homonym *Gobius viridis* Otto, 1821. Koumans (1953, p. 263) noted this but continued to use the name *viridis*, apparently unaware that as a junior primary homonym it should be permanently rejected (*International Code, Article* 59 (*a*)).

76. " ***Triacanthus biaculeatus*** "
= ***Triacanthus biaculeatus*** (Bloch, 1786)

Two fishes, 35·7 and 118·2 mm. S.L. (the larger fish 149 mm. tot. l.), in good condition, with modern label " *Triacanthus brevirostris* China Vachell " (following the catalogue entry), UMZC. VIII, 209.

DESCRIPTION. (based on the larger of the two fishes). D_1 IV, D_2 22, P i 14, V I, A 18.

In percentages of standard length : body depth 42·5, head length (to upper limit of gill opening) 29·8 ; snout length 19·2, eye diameter 8·0 ; pectoral length 10·3, pelvic length 22·0, 1st dorsal spine length 26·7 ; length of 2nd dorsal fin base 25·5, length of anal base 17·9 ; pre-dorsal distance 42·5, pre-pelvic distance 34·7, pre-anal distance 62·4 ; caudal peduncle, length 22·7, depth (greatest) 12·2, (least) 4·6.

Body depth equal to pre-dorsal distance. Snout slightly concave in profile. Interorbital space slightly concave but with low median ridge. First dorsal spine 9/10 of head length ; second dorsal spine 3/10 length of first spine ; following spines decreasing in length. Distance between the last ray of the first dorsal and the origin of the second dorsal 1·4 times eye diameter. Longest rays of the second dorsal 9/10 eye diameter. Base of second dorsal 1·43 times in base of anal. Pectoral fins rounded, their length $\frac{2}{3}$ of distance between eye and base of first dorsal spine. Pelvic bone between pelvic spines tapering to a point. Caudal forked. Caudal peduncle tapering to base of caudal, its length 4·4 times in standard length, its greatest depth 1·86 times in its length.

Colour: body light brown ; basal part of first dorsal spine, and membrane between first three dorsal spines, speckled with light brown and edge of fin membrane in this area dark brown.

Note: the concave snout profile and the pointed pelvic bone places this specimen in *T. biaculeatus*, not *T. brevirostris* as the label on the jar indicates. The descriptions and key of De Beaufort & Briggs (1962) have been used, but they do not indicate what changes can be expected with age ; the two species are otherwise very similar. Richardson (1846, p. 202) does not list any Vachell material, but the present specimens may have been overlooked.

The final (5th) spine in the first dorsal fin is missing (?concealed) in the larger specimen, a character used by Fraser-Brunner (1941) in his diagnosis of the subgenus *Triacanthus* (*Trixiphichthys*) Fraser-Brunner (type and only species, *Triacanthus weberi* Chaudhuri). The present specimen differs from *T. weberi* in having the normal snout (greatly compressed and pointed in *T. weberi*). Dr. J. Tyler informs us (pers. comm.) that the 5th and 6th spines of the first dorsal may lie below the surface in *Triacanthus* but can be found by staining.

79. " ***Tetrodon ocellatus*** "

= ***Fugu (Torafugu) ocellatus*** (Linneaus, 1758)

A single fish, 102 mm. S.L. (127 mm. tot. l.), mounted for exhibition in " perspex " box with modern label " *Tetrodon ocellatus* " but with no indication of locality or donor, UMZC. F.4227 (catalogued without donor or locality).

This fish could have been part of the Cambridge Philosophical Society collection, but Harmer evidently did not consider that it was part of the Vachell collection, nor does Richardson mention Vachell material (see above, p. 147).

In his review of the puffer fish genera, Fraser-Brunner (1943) employed the genus *Torquigener* Whitley, 1930 for this species, which had otherwise been placed in the compendium genus *Sphaeroides*. However, Abe (1952) showed this to be incorrect, and proposed the genus *Fugu* for Japanese members of the genus *Sphaeroides*. Chu, Tchang & Chen (1963) agreed, and we have followed these authors here.

80. " ***Echeneis naucrates*** "

= ***Echeneis naucrates*** Linnaeus, 1758

One extant fish, 280 mm. tot. l., mounted for exhibition in " perspex " box with modern label " *Echeneis naucrates* ", but with no indication of locality or donor, UMZC. F.2917 (catalogued as China Seas. Cambridge Philosl. Society's Colln.). (A smaller fish, 115 mm. tot. l., *ex* Borneo, is mounted in the same box.)

Richardson mentions a British Museum specimen, but no Cambridge material, even though the present specimen is listed by Harmer as coming from the Cambridge Philosophical Society's collections. The specimen can be regarded as possibly part of the Vachell collection.

Table I

Richardson species based on Vachell material

	Richardson species	Name accepted here	Richard. Report Page No.	Reeves illustr. No.	Reeves Page No.
4*	†*Chatoessus maculatus*	*Clupanodon thrissa*	308	109	91
7	*Anguilla clathrata*	*Anguilla japonica*	312	—	—
11	*Bagrus vachellii*	*Pseudobagrus vachellii*	284	—	—
12	*Bagrus limbatus*	*Pelteobagrus fulvidraco*	283	—	—
15	*Solea ovata*	*Microbuglossus ovatus*	279	—	—
16	†*Solea ommatura*	*Zebrias zebra*	279	β13	71
17	*Plagiusa grammica*	*Cynoglossus grammicus*	280	—	—
24	†*Trachinotus melo*	*Psenopsis anomala*	270	97	68
25	*Seserinus vachellii*	*Parastromateus niger*	273	—	—
28	†*Caranx cancroides*	*Caranx* (*Atule*) *kalla*	274	β30	35
33	*Ambassis vachellii*	*Ambassis commersonii*	221	—	—
35	†*Serranus shihpan*	*Epinephelus akaara*	231	71	14
36	†*Priacanthus tayenus*	*Priacanthus tayenus*	237	β14	71
53	†*Sebastes vachellii*	*Sebastodes vachellii*	214	69?	14
54	†*Pelor tigrinum*	*Inimicus japonicus*	212	β42	28
60	†*Julis exornatus*	*Halichoeres nigrescens*	258	β10	56
62	†*Gobius platycephalus*	*Glossogobius brunneus*	204	L94	124
64	*Gobius margariturus*	*Rhinogobius margariturus*	205	—	—
65	*Gobius ripilepis*	*Drombus ripilepis*	205	—	—
66	*Gobius stigmothonus*	*Acanthogobius stigmothonus*	205	—	—
67	†*Apocryptes serperaster*	*Apocryptes serperaster*	206	β55	96
77	*Balistes vachellii*	*Abalistes stellatus*	201	—	—

* Number as listed in text.
† Reeves illustration reproduced here.

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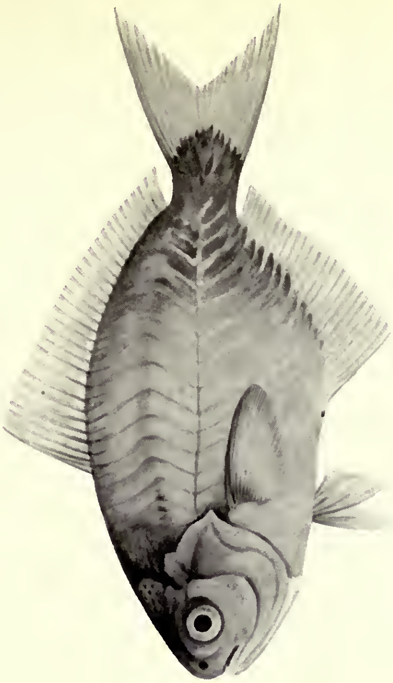
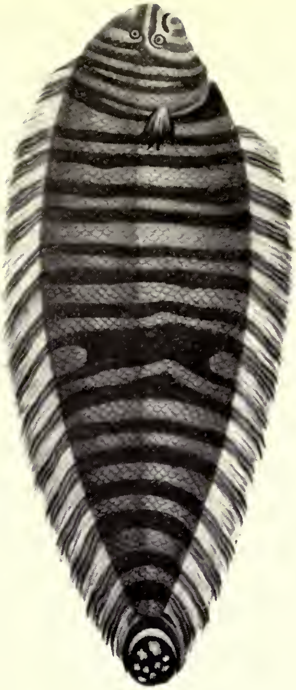
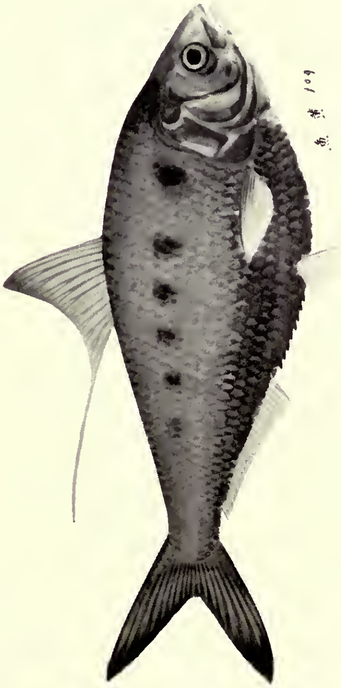
PLATE 1

FIG. 1. *Chatoessus maculatus* (=*Clupanodon thrissa*). Reeves p. 91, No. 109.
FIG. 2. *Caranx cancroides* (=*Caranx* (*Atule*) *kalla*). Reeves p. 35, No. β30.
FIG. 3. *Trachinotus melo* (=*Psenopsis anomala*). Reeves p. 68, No. 97.
FIG. 4. *Solea ommatura* (=*Zebrias zebra*). Reeves p. 71, No. β13.



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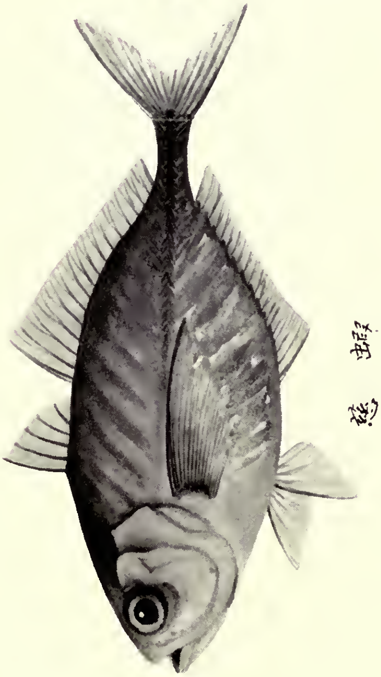
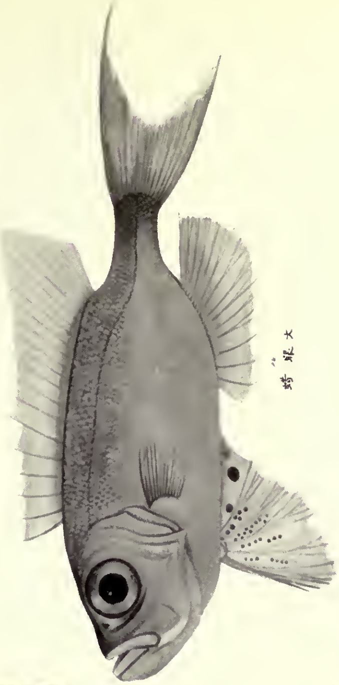


PLATE 2

Fig. 1. *Serranus shihpan* (=*Epinephelus akaara*). Reeves p. 14, No. 71.

Fig. 2. *Priacanthus tayenus* (=*Priacanthus tayenus*). Reeves p. 71, No. *β*14.

Fig. 3. *Sebastes vachellii* (=*Sebastodes vachellii*). Reeves p. 14, No. 69.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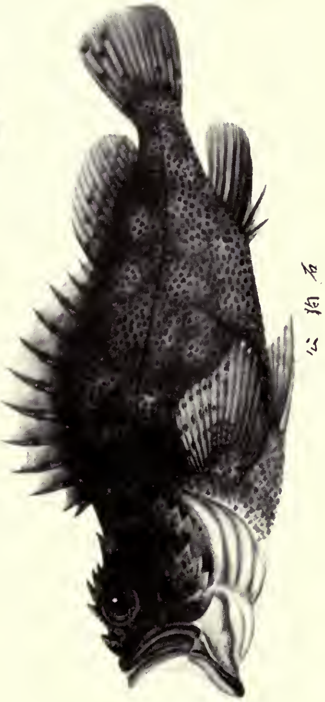
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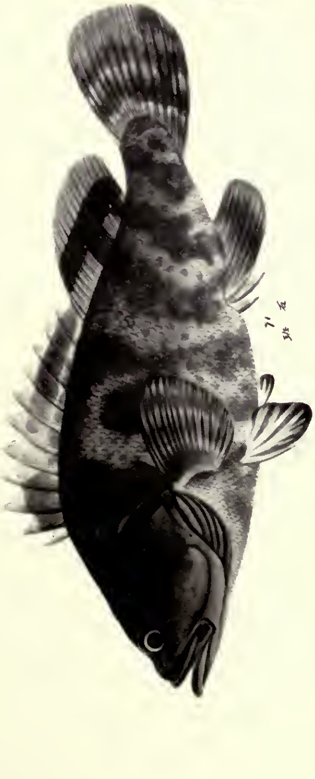
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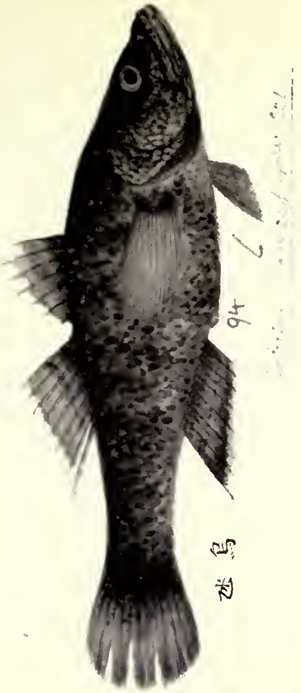
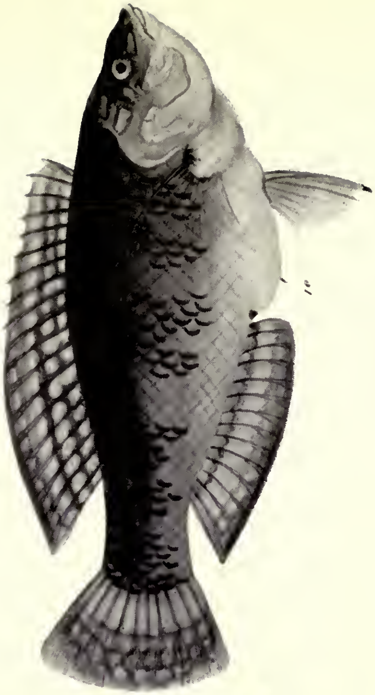
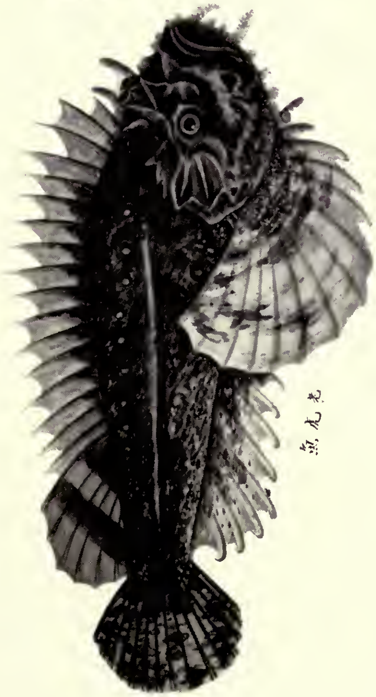
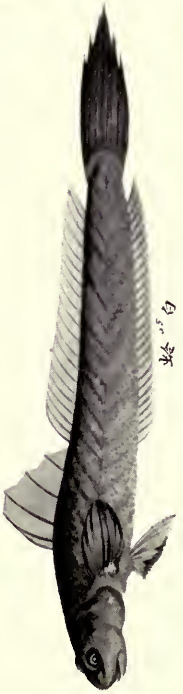
PLATE 3

FIG. 1. *Pelor tigrinum* (=*Inimicus japonicus*). Reeves p. 28, No. β42.
FIG. 2. *Apocryptes serperaster* (=*Apocryptes serperaster*). Reeves p. 96, No. β55.
FIG. 3. *Gobius platycephalus* (=*Glossogobius brunneus*). Reeves p. 124, No. 194.
FIG. 4. *Julis exornatus* (=*Halichoeres nigrescens*). Reeves p. 56, No. β10.









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V. *NARDOA* AND SOME OTHER OPHIDIASTERIDS

AILSA McGOWN CLARK

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ZOOLOGY Vol. 15 No. 4
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British Museum (Natural History)

Pp. 167–198 ; 6 *Plates*

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NOTES ON ASTEROIDS IN THE BRITISH MUSEUM (NATURAL HISTORY)
V. *NARDOA* AND SOME OTHER OPHIDIASTERIDS

By AILSA McGOWN CLARK

THE present study includes notes on the provenance of *Nardoa variolata* (Lamarck) the type-species of *Nardoa*, details of the true holotype of *N. gomophia* (Perrier), description of a new species from northern Australia and a discussion of the remaining species of the genus coupled with notes on the validity of the monotypic *Gomophia*, a new subspecies of which is described.

In the course of this, the following conclusions are reached :—

Ophidiaster watsoni Livingstone (1936) is referred to *Gomophia* and is probably conspecific with *G. egyptiaca*

Nardoa mamillifera Livingstone (1930) and *N. tumulosa* Fisher (1917) are probably synonyms of *N. frianti* Koehler

Nardoa obtusa (Perrier) is conspecific with *N. tuberculata* Gray

Nardoa lemonnieri Koehler is revived from the synonymy of *N. mollis* de Loriol and

Nardoa faouzii Macan is designated as type-species of a new subgenus.

A key to the species of *Nardoa* is included.

Other Ophidiasterids dealt with include :—

Fromia indica (Perrier), with *F. tumida* Bell newly referred to synonymy but *F. elegans* H. L. Clark revived as a valid species

A new species of *Fromia* from the Indian Ocean.

Ferdina Gray, re-diagnosed and restricted to a monotypic genus by removal of *F. heffernani* Livingstone to a new genus ; *Ferdina flavescens* Gray partially redescribed

Tamaria tumescens (Koehler), with *T. ajax* Livingstone, 1932*a*, newly referred to synonymy and

Ophidiaster helicostichus Sladen now referred back to *Ophidiaster* from *Hacelia* with possible synonym *O. astridae* Engel, 1938.

Gomophia egyptiaca egeriae[1] subsp. nov.

(Pl. 1, figs. 1–5)

Nardoa tuberculata (pt.) Bell, 1894 : 396.
? *Nardoa aegyptiaca* : Koehler, 1910 : 157 [Non *Gomophia egyptiaca* Gray].

MATERIAL. Macclesfield Bank, South China Sea ; Admiralty :—23 metres, 2 specimens—the holotype and paratype, B.M. reg. no. 92.8.22.52 and 53 ; 66–76 metres, 3 specimens, nos. 92.8.22.74, 259 and 260 ; 58 metres, 1 specimen, no. 92.8.22.29 ; 76–84 metres, 1 specimen, no. 93.8.25.203.

---

[1] Named after H.M.S. " Egeria " which surveyed Macclesfield Bank.

Description of holotype. R/r = 70 mm./11·5 mm. = 6·1/1. The arms taper fairly evenly to attenuated tips ; br at the base = 10·5 mm., at half R = 9·0 mm. and at 10 mm. from the tip = 4·0 mm.

The aboral skeleton is reticulate but the oblong secondary plates linking the five- or six-lobed primary abactinal ones are relatively inconspicuous and the reticulum is more compact than in the holotype of *G. egyptiaca egyptiaca*, the pore-areas being relatively small, mostly with only 3–6 pores in each. Three plates around the centre of the disc and fifteen to twenty other primary ones scattered along the upper side of each arm are abruptly elevated, the larger ones 2·4–2·6 mm. in basal diameter and 2·0–2·4 mm. in height. Their shape is conical but some have the apex blunted.

The supero-marginal series of plates similarly includes both flat and markedly convex plates, the former being mostly equal in size to the largest of the flat abactinal plates. The convex plates arise at intervals of one to four flat ones, and are more widely-spaced on the distal half of the arm.

The entire surface is coated with fine granules concealing the underlying plates. On the flatter parts of the aboral skeleton these number c. 60/sq. mm. but on the convexities they become distinctly coarser, especially towards the tips of the plates. Most of these tips have been rubbed but on those that remain intact the apex is crowned by several enlarged granules among which a single central one may reach twice the diameter of the granules encircling it. Though slightly higher than the other granules, this single one is throughout too small to evoke comparison with a nipple. It is more often developed on the supero-marginal plates than the abactinal ones.

The infero-marginal plates form a much more regular series than the supero-marginals, all being similar and gradually reducing in size distally ; the proximal ones are conspicuous by their size and measure almost 3 mm. in diameter. The number in one series partially denuded is c. 30.

Between the two main marginal series proximally is a row of intermarginal plates. Beyond the basal third of the arm length these are concealed by the granulation but spaced ones are revealed on the denuded arm to c. half R. Small pore-areas are present both above and below the intermarginal plates continuing distally beyond them but there are none on the lower surface of the body below the infero-marginals.

The actinal series of plates is poorly developed, the one cleared consisting of 18 plates, about three corresponding to each infero-marginal where they lie adjacent ; the distalmost actinal plate lies interstitially between the seventh and eighth infero-marginals and the adjoining adambulacrals, i.e. at just over one-third R from the mouth.

The adambulacral plates for much of the arm each bear four, rarely five, prismatic furrow spines c. 1 mm. long, the fans of which are slightly oblique so that consecutive ones tend to overlap. Behind these are series of usually three shorter subambulacral spines, the middle one becoming progressively stouter and relatively longer on the distal part of the arm, while the proximal one disappears or becomes granuliform. The outer part of the plate bears polygonal granules indistinguishable from those of the adjacent actinal and infero-marginal plates so that the two rows of spines project abruptly. In comparison with the species of *Nardoa*, the adambulacral spines are more slender and spaced farther apart.

Paratypes. [Treated in the same order as in table 1 on p. 177]. As indicated in the table, the raised abactinal and supero-marginal plates are more or less rounded at the tips and may lack the single enlarged granule altogether. In the specimen from the same depth as the holotype (R 65 mm., Pl. 1, fig. 4) the enlargement of the supero-marginal plates is more frequent, there being a marked tendency for every second one to be convex. In this specimen the furrow spines number five on most of the plates of the proximal half of the arm ; also the granules adjacent to the subambulacral spines are slightly elongated.

No. 93.8.25.203 (R 70 mm.) has alternate proximal supero-marginal plates tubercular but distally the frequency of these is less. Again there are five furrow spines on most of the proximal plates.

No. 92.8.22.29 (R 60 mm.) has very regular alternation of convex and flat supero-marginals for almost the entire length of all the arms. There are four, occasionally five, furrow spines.

In no. 92.8.22.74 (R 52 mm.) the single apical granule of some of the supero-marginal plates at least (most of the aboral ones being rubbed) approaches nipple-like proportions. The furrow spines usually number four.

Finally, nos. 92.8.22.259 and 260 are smaller, R 34 and 32 mm. (The latter has only two arms intact and is not included in the Table). The former (Pl. 1, fig. 5) has markedly conical tubercular plates, of which the two midradial ones near the base of each arm are so large as almost to meet the supero-marginal plates each side, only one small flat plate intervening. This is in marked contrast to the specimens of *G. egyptiaca egyptiaca* of similar size from Christmas Island, where the abactinal plates are relatively smaller and more numerous (Pl. 1, fig. 6). Another difference is that the intermarginal plates are very narrow in the Macclesfield Bank specimen and indeed are only visible when the granulation is removed, being sandwiched closely between the two main marginal series. The Christmas Island specimens have conspicuous broad series of intermarginal plates extending for about half R. However, the two from Macclesfield Bank cannot be referred to *Nardoa frianti* since they both have unusually well-developed, almost nipple-sized and sharp apical tubercles on the conical abactinal and supero-marginal plates. It may be noted that a few of the supero-marginals are crowned by two or even three tubercles, which may also occur in *G. egyptiaca egyptiaca*, as shown by a specimen from Samoa (poorly preserved and not included in Table 1) though here the tubercular plates tend to have a double apex like a cow-bell and the tubercles are separated at the ends of the ridge.

Comparative remarks between *egeriae* and *egyptiaca* as well as with *Nardoa* are included in the general discussion of *Nardoa* and *Gomophia*.

Nardoa variolata (Retzius)

Tetractis cruciata variolata Linck, 1733 : 19, pl. i, no. 1.
Pentadactylosaster variolatus Linck, 1733 : 34, pl. viii, no. 10.
Hexactis variolata Linck, 1733 : 37, pl. xiv, no. 24.

[Un-named] Encyclopedie Méthodique, 1792 : pl. cxix, figs. 4, 5 [" *Asterias variolata* : Lamarck " in captions, 1827].
Asterias variolata Retzius, 1805 : 19 ; Lamarck, 1816 : 565.
Linkia variolosa (sic) : Nardo, 1834 : 717.
Nardoa variolata : Gray, 1840 : 286 ; 1866 : 15 ; Fisher, 1919 : 379, pl. cviii, fig. 4 ; H. L. Clark, 1921 : 51, pl. xxviii, figs. 3, 4. [Non Domantay & Roxas, 1938 : 224–225, probably = *N. novaecaledoniae*].
Nardoa Agassizii Gray, 1840 : 287 ; 1866 : 15.
Scytaster variolatus : Müller & Troschel, 1842 : 34–35 ; Michelin, 1845 : 21 ; Peters, 1852 : 178 ; Lütken, 1865 : 41 ; Perrier, 1875 : 159–162 (423–426) ; Smith, 1879 : 566 ; Möbius, 1880 : 50 ; de Loriol, 1885 : 43–44. [Non Bell, 1882 : 220 ; 1887 : 647 ; ?1902 : 226 ; ?1909 : 19].

This species was formally designated as type-species of *Nardoa* by H. L. Clark (1921). Unfortunately, although there has long been agreement that the common *Nardoa* of Mauritius should be called *variolata*, the basis for this is not perfectly secure since no holotype is extant. One solution would be for a neotype to be chosen. Alternatively a lectotype could be selected from among Linck's figures (1733) which were cited by Retzius, the first post-Linnean author to use and thereby validate the name. As Linck's specimens are not preserved at the present museum in Trier the figures alone will have to suffice. Those of the normal five-armed specimen (Linck, pl. viii, no. 10) reproduced in the " Encyclopedie Méthodique", are to be preferred; they certainly have a strong resemblance to the common *Nardoa* of Mauritius. Linck, Retzius and Nardo all failed to give a locality for the species but Lamarck put " mers d'Europe " from which Gray appears to have derived " Mediterranean Sea " at the same time as he gave " Isle of France " (Mauritius) for *Nardoa Agassizii*, subsequently referred to the synonymy of *variolata* by Müller and Troschel, who also record specimens from Mauritius.

Some remarks about the geographical and morphological limits of the species are included in the general discussion of *Nardoa*.

Nardoa gomophia (Perrier)

(Pl. 2, figs. 1–4)

Scytaster gomophia Perrier, 1875 : 167–169 (431–433). [Non *Nardoa* " *gamophia* " : Fisher, 1919 : 380, which is based on a specimen of *N. novaecaledoniae*].

MATERIAL. New Caledonia ; Cuming ; the holotype, B.M. reg. no. 59.4.25.3.

As Fisher noted in 1919, the specimen (Pl. 5, fig. 2) in the British Museum collections hitherto labelled as the holotype of Perrier's *Scytaster gomophia* does not particularly resemble *Gomophia egyptiaca* with which Perrier allied and compared his new species but is close to *Nardoa novaecaledoniae.* Its number is 59.4.25.4 and a search through the dry collections yielded a second specimen not conspecific with the first but also labelled as from New Caledonia and having the consecutive number 59.4.25.3 (Pl. 2, figs. 1–4). This specimen bears a label " *Scytaster* n. sp. ", though not in Perrier's handwriting. A later printed label names it *Nardoa perrieri*, which I think must be an MS name given it by Bell prior to placing it on exhibition. This second specimen does have a considerable resemblance to *Gomophia egyptiaca* owing to the presence of some spaced, abruptly projecting, tubercular plates on the upper side. As in Perrier's description, these are hemispherical rather than conical, unlike *G. egyptiaca*, and tend to form three alternating series along each arm. No such projections are present in the first specimen, 59.4.25.4, but this does agree in diameter with Perrier's measurement of 135 mm., the mean of its five possible diameters being 131 mm., whereas the same mean in no. 59.4.25.3 is 167 mm. However, the R/r ratio of 7·7/1 in the latter compared with 5·5/1 in no. 4 agrees so closely with Perrier's estimate of " nearly 8/1 " that I am convinced the wrong specimen has been labelled as the holotype of *N. gomophia*. Accordingly the assessment of the species must be reviewed since H. L. Clark referred *gomophia* to the synonymy of *N. novaecaledoniae* following Fisher's comments. On the one hand it is clearly related to those species of *Nardoa* which have some of the abactinal plates distinctly tubercular and on the other to *Gomophia egyptiaca*, as Perrier stated. To avoid repetition, the comparison is included in the general discussion of *Nardoa* and *Gomophia*.

Nardoa sphenisci[1] sp. nov.

(Pl. 3, figs. 1–3)

MATERIAL. Holothuria Bank, N.W. Australia, 27 metres ; H.M.S. " Penguin ". 1 specimen, the holotype, B.M. reg. no. 92.1.14.27.

Parry Shoal (N.W. of Darwin), 22 metres ; H.M.S. " Penguin ". 2 specimens, no. 92.4.4.6 and 7.

DESCRIPTION OF THE HOLOTYPE. R 115–120 mm. ; r c. 13 mm. ; R/r = 9·0/1. The arms are slender and attenuated, br at the base = 13–14 mm., at half R = c. 10 mm., at 10 mm. from the tip = 4·5–5·0 mm. and at the very tip = c. 2 mm. One arm has been broken near the base and is regenerating.

Most of the abactinal plates are more or less convex, especially the midradial ones near the bases of the arms, which are 2·5–3·5 mm. in transverse diameter (slightly less longitudinally) and up to 1·5 mm. in height ; their tops are rounded. Beyond the bases of the arms the more convex plates are scattered over the whole upper side. Across the base of each arm between the two supero-marginal series the abactinal plates number five to seven ; when there are seven the two outermost plates are small, for most of the proximal part of the arm there are about five plates across the width though the arrangement is irregular. Distally the plates gradually decrease in size and become elongated, the more convex ones measuring 2·0–2·5 mm. in length and 1·0–1·5 mm. in breadth. Only on the regenerating arm is there an abrupt reduction in the size of the plates at the point of cleavage.

The entire aboral surface is coated with polygonal granules which gradually increase in size on the convexities of the skeleton. The smaller granules between and towards the edges of the plates number 25–30 per square mm. ; they are flat-topped and each granule bears a small boss in the centre except for the coarser ones near the apices of the more conical plates, which tend to have their whole free surface convex and smooth. The smaller distal convex plates particularly have the few enlarged central granules distinctly projecting and on some of these plates there is one central granule which is markedly larger than the seven or eight immediately encircling it. This gives a rough texture to the distal parts of the arms although the central granules are barely visible with the naked eye and never so abruptly different from the other granules as to recall the nipple-like tubercles found on the swollen plates of most specimens of *Gomophia egyptiaca*.

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[1] Of the " Penguin ".

The supero-marginal plates also are more or less convex in form though never to the same extent as the proximal mid-radial plates. There is a strong tendency for alternate supero-marginals beyond the basal five to ten to be larger and more convex than the rest so that the outline of the arms in perpendicular view is distinctly and fairly regularly scalloped. The larger plates of the basal half of the arm are 2·0–2·5 mm. in diameter, the alternate plates being only c. 1·0 mm. long though still c. 2 mm. wide. In two supero-marginal series counted the total number of plates is 58.

In contrast the infero-marginal plates are fairly equal in size, gradually diminishing distally. They number c. 54.

Both series of marginal plates are covered with granulation similar to that on the abactinal plates ; this again becomes increasingly coarse on the more convex surfaces. On some of the distalmost plates of both series when only a single granule is enlarged the height of this may exceed its basal breadth though the tip is rounded.

In each interradius the two marginal series are separated by a progressively narrowing series of irregularly-placed and irregularly-shaped intermarginal plates. On one area cleared these number about 40 and extend for c. 40 mm. along the arm, although when the granule-covering was intact the plates of the distal half of the series were concealed.

On the lower side, the main series of actinal plates is visible through the covering granulation for about half the arm length, (i.e. to about the twenty-fifth infero-marginal) ; further plates extend interstitially concealed by the granulation to about the thirty-fifth infero-marginal or two-thirds of the arm length. The actinal plates are twice as numerous as the adjoining infero-marginals. On the disc there is a second series consisting of only two or three plates. The granulation is again coarser on the centres of the plates than around their edges.

The adambulacral plates correspond in number to the actinal plates. Each bears four or five blunt angular furrow spines, the distal plates more often four, though the number may be only three on the terminal fifth of the arm. When there are five furrow spines, usually the proximalmost one is slightly smaller than the rest and inset from the furrow so that the series is curved and adjacent ones tend to overlap. The subambulacral row consists usually of three spines, shorter but somewhat stouter than the furrow spines and often with a smaller fourth proximal spine almost in series with them. The outer part of the plate bears polygonal granules some of which, close behind the subambulacral spines are slightly elongated so that there is no abrupt transition from spines to granules.

The pore-areas are small in comparison to the size of the plates. The number of pores in each area is difficult to estimate, perhaps owing to the dried condition ;

on the upper side it is probably 4–8 in most areas. Smaller pore-areas are also present intermarginally and below the infero-marginals on the proximal half of the arm.

PARATYPES. Both have R/r 75–85 mm./10 mm., approximately 8/1. The arms are slender and attenuated as in the holotype, which they closely resemble. Both have the intermarginal series of plates well-developed on most arms and only lacking on those arms which appear to have regenerated from the base. This can be assumed from the abrupt break in all three marginal series close to the interradius and to coincidence in the occurrence of intermarginal series on both sides of a single arm rather than on the two continuous series of adjacent arms across an interradius. The actinal plates are more extensive than in the holotype, being visible for about five-eighths R with further plates extending to three-quarters R concealed to the naked eye beneath the granulation. The furrow spines number four on most plates of the proximal half of the arm, then three.

REMARKS. All three specimens were identified as *Nardoa tuberculata* by Bell. In 1953 I re-named them *Gomophia egyptiaca* on account of the intermarginal series of plates and the attenuated arms, disregarding the rounded rather than conical tubercular abactinal plates lacking in central conical nipples. However, a recent study of material of these two genera convinces me that the three specimens are referable to neither species. Their relationships are dealt with below in the general discussion of *Nardoa* and *Gomophia*.

NARDOA Gray

Gray, 1840 : 268 ; 1866 : 15 ; Fisher, 1919 : 378–382 ; H. L. Clark, 1921 : 49–50.

The species of *Nardoa* are usually divided into two groups, those in which some of the abactinal plates are distinctly more convex than the rest and those with similar low plates. The relationship between the first group and the monotypic genus *Gomophia* should be reviewed, the latter having been referred to the synonymy of *Nardoa* by several specialists including Sladen (1889), Koehler (1910) and Fisher (1919) but restored to generic rank by H. L. Clark (1921) and following workers.

Unfortunately, most of the species involved seem to be solitary and the available samples are very inadequate, rarely more than one or two specimens being taken at a time so that the range of variation is poorly known. Following the restoration here of *N. gomophia* as a valid species and the addition of *N. sphenisci* as a new one, the nominal species to be included in such a survey are :—

Gomophia egyptiaca Gray, 1840
" *Ophidiaster* " *watsoni* Livingstone, 1936
Nardoa frianti Koehler, 1910
Nardoa tumulosa Fisher, 1917
Nardoa mamillifera Livingstone, 1930
Nardoa gomophia (Perrier), 1875
Nardoa sphenisci sp. nov.

Nardoa tuberculata Gray, 1840
Nardoa obtusa (Perrier), 1875 and possibly also
Nardoa rosea H. L. Clark, 1921.

Some of the distinguishing characters between these are brought out by the following table. In this the skeletal structure is indicated as either open, when the papular areas are sufficiently large to give a reticular appearance, as opposed to compact, with the spaces small and irregular in arrangement. A comparison of Pl. 1 figs. 1 and 3 with 6 and 8 may serve to illustrate this point). Negative entries for the abactinal tubercles signify that they are conical. The degree of fineness of the covering granulation is shown by an assessment of the number per square mm. taken on the flatter parts of the aboral skeleton where the granulation is at its finest. The other columns should be self evident. Intermediate conditions are indicated by " +/— " and a tendency one way or infrequent occurrence by brackets.

H. L. Clark distinguished *Gomophia* from *Nardoa* by the unspecialized supero-marginal plates resembling the abactinal ones (this being enhanced by the series of intermarginal plates separating the supero-marginals from the markedly enlarged infero-marginals proximally) and by the absence of actinal papulae below the infero-marginals (this character implicit in his key) coupled with the conical form and apical " nipples " of the tubercular abactinal plates ; an additional distinction is provided by the rather open, apparently reticulate, aboral skeleton.

However, although in the holotype of **Gomophia egyptiaca** and in a few other specimens closely resembling it, notably the one from Samoa shown in Pl. 1, figs. 7 and 8, none of the supero-marginal plates are enlarged or projecting, this is not always the case ; for instance the fine large specimen from the Gulf of Aqaba (see A. M. Clark, 1952), the second one in the table, has a conspicuous conical tubercular plate in the position of every third or fourth supero-marginal. Similarly some much smaller specimens from Christmas Island in the Indian Ocean have some elevated supero-marginals; in this case alternate plates are so modified, as in the holotype of Livingstone's **Ophidiaster watsoni** to which the Christmas Island specimens bear great resemblance. In fact, despite the extent of some of the actinal series of plates beyond half the arm length and the slight enlargement of the granules adjoining the subambulacral spines, I have no hesitation in declaring *O. watsoni* to be congeneric, possibly even conspecific, with *Gomophia egyptiaca*. It is significant that Endean (1965) has recorded *G. egyptiaca* from Queensland.

Seven specimens from Macclesfield Bank, South China Sea, which I have referred to *Gomophia*, also have some of the supero-marginals, often alternate ones, tubercular ; such a frequency of the tubercular plates coupled with their linear arrangement gives a greater appearance of specialization to the supero-marginals than is evident in the holotype of *G. egyptiaca*. Bell included these China Sea specimens, together with three others which I believe are *Nardoa frianti*, in *N. tuberculata*. However, the presence of intermarginal series of plates, the much more prominent tubercular plates of the aboral side often crowned with enlarged granules or even a single small tubercle, the absence of actinal papulae, the reduction of the actinal series of plates and the abrupt transition from the granulation of the lower side to

TABLE I.

Species	Locality	R (mm.)	Skeleton open	Tubercles rounded	Nipples present	Arms blunt-tipped	Some s.m. plates tubercular	Inter-marginal plates present	Actinal plates extent /R	Actinal papulae present	Interstitial granulation no./sq. mm. (approx.)	Adambulacral armament graduated
Gomophia egyptiaca T	Red Sea	65	+	–	+	–	–	+	c. $\frac{1}{2}$	–	110	–
,, ,,	,, ,,	90	+	–	+	–	(+)	+	$<\frac{1}{2}$	–	90	–
,, ,,	Samoa	50	+	–	+	(–)	–	+	$<\frac{1}{2}$	–	90	–
,, ,,	Mauritius	35	+	–	+	(–)	–	+	$<\frac{1}{2}$	–	85	–
,, ,,	Loyalty Is.	43	–	–	+	+/–	+	+	$<\frac{1}{2}$	–	100	+/–
,, ,,	Christmas I.	32	+	–	+	(+)	+	+	c. $\frac{1}{2}$	–	100	–
" *Ophid. watsoni* " T	Queensland	50	+	–	+	(+)	+	+	$\frac{1}{2}$–$\frac{2}{3}$†	–	" minute "	+
G. e. egeriae T	Macc. Bank	70	–	+/–	(+)	–	+	+	$<\frac{1}{2}$	–	60	–
,, ,, ,,	,, ,,	65	–	+	–	–	+	+	$<\frac{1}{2}$	–	70	+/–
,, ,, ,,	,, ,,	70	–	+	–	–	+	+	$<\frac{1}{2}$	–	70	–
,, ,, ,,	,, ,,	60	–	+/(–)	(+)	–	+	+	$<\frac{1}{2}$	–	75	+/–
,, ,, ,,	,, ,,	52	–	+/–	(+)	–	+	+	$<\frac{1}{2}$	–	66	–
,, ,, ,,	,, ,,	34	–	–	+	–	+	+	$<\frac{1}{2}$	–	75	+/–
Nardoa frianti T	Andaman Is.	95	–	+	–	–	+?	(+)/–	c. $\frac{1}{2}$	–	–	–
,, ,, : Fisher	Sulu Arch.	126	–	+	–	–	?	?	?	+	–	?
,, ,,	Macc. Bank	72	–	+/–	–	–	(+)	–	$\frac{2}{3}$–$\frac{3}{4}$	+	48	+
,, ,,	,, ,,	85	(–)	+/–	(+)/–	–	+	–	$\frac{1}{2}$–$\frac{2}{3}$	+	60	+
,, ,,	,, ,,	90	(–)	+	–	–	+	–	$\frac{2}{3}$–$\frac{3}{4}$	(+)	55	+
,, ,,	Loyalty Is.	65	(–)	+	–	+	+	–	c. $\frac{7}{8}$	+	36	+
,, ,, *C	,, ,,	55	(–)	+	–	+	+	–	c. $\frac{3}{4}$	+	50	+/(–)
N. mamillifera T	Queensland	63	–?	+	–	+	+?	?	c. $\frac{3}{4}$†	+?	–	+
N. rosea : Liv.	,,	88‡	–	+	–	–	+	–	$\frac{1}{2}$–$\frac{2}{3}$	+	33	+
N. tumulosa : Hay.	Ryu Kyu Is.	65	–?	+	–	–	+?	–	?	?	–	?
,, ,, T	Sulu Arch.	90	(–)	+	–	–	–	(+)	c. $\frac{1}{3}$	–	–	+
,, ,, : Hay.	Carolines	54	?	+	–	–	?	–	c. $\frac{7}{8}$	+	–	?
N. gomophia T	New Caledonia	92	(–)	+	–	–	+	–	c. $\frac{3}{4}$	+	35	+
N. tuberculata T	Philippines	82	–	+	–	+	–	–	$\frac{7}{8}$+	+	25	+
N. sphenisci T	N. Australia	118	–	+	–	–	+	+	$\frac{2}{3}$	+	28	+

* C signifies a specimen from the Cambridge Museum collection.

† These estimates are derived from Livingstone's photographs as his descriptions of the actinal (or actino-lateral) plates are confused.

‡ Livingstone gives R as only 72 mm. but the " string-along-furrow " method of measurement gives c. 88 mm. on all four intact arms.

the two rows of adambulacral spines all agree with *G. egyptiaca*. Nevertheless, when the fine coat of granules is removed from the upper side, the underlying skeleton appears to be much more compact in these specimens from Macclesfield Bank than in the others included in the table from the Red Sea, Mauritius, Samoa and Christmas Island. Possibly this can be attributed in some degree to contraction in preservation since an unnaturally flattened specimen from Eilat in the Red Sea similarly shows compaction of the abactinal skeleton. The more or less rounded form of the swollen abactinal and supero-marginal plates in most of the specimens from Macclesfield Bank, coupled with the poor development of the apical nipples (these often being confined to the supero-marginals) provides another distinction and three of the specimens have a slight transition from the granulation of the lower side to the subambulacral spines. Also the granulation of the abactinal plates seems to be slightly coarser than in those specimens of *G. egyptiaca* which most resemble the holotype. I do not consider that these differences carry sufficient weight to merit more than a subspecific distinction for the Macclesfield Bank specimens which are accordingly described here as *Gomophia egyptiaca egeriae*.

The relative specialization of their supero-marginal plates weakens the generic distinction of *Gomophia* on the basis of this character. Of the other supposedly diagnostic characters, the absence of actinal papulae is certainly constant in *G. egyptiaca* but unfortunately is matched by individuals of several species of *Nardoa*, for instance the types of both **Nardoa frianti** and **Nardoa tumulosa,** also the specimen from the Ogasawara (Bonin) Islands referred to *frianti* by Hayashi (1938*b*) ; certainly the actinal papulae are few and inconspicuous in the specimens from Macclesfield Bank which I have attributed to *frianti*.

As for the occurrence of intermarginal plates, these are not restricted to *G. egyptiaca*. Fisher notes that there are a few intermarginal plates at the base of each arm of the holotype of *N. tumulosa*, while Koehler writes to the effect that in the two syntypes of *N. frianti* " sometimes the two marginal series are fully contiguous but sometimes there are small plates intercalated between them, though these rarely form a regular and distinct series but rather are inserted in the intervals between the larger plates ". No such intercalary intermarginals are developed in the Macclesfield Bank specimens of *Nardoa*, while Hayashi (1938 and 1938*a*) mentions only intermarginal papulae, not plates, in the specimens from the Caroline and Ryu Kyu Islands which he referred to *N. tumulosa*. However, the specimen from the Ogasawara Islands (Hayashi, 1938*b*), figured under the name of *N. frianti*, not only has well-developed series of intermarginal plates but also has the tubercular abactinal plates restricted to the proximal parts of the arms (like Hayasaka's specimen from Taiwan [Formosa], 1949, Pl. ii, fig. 4, named *tumulosa*), combining to give it a strong resemblance to the holotype of *N. tumulosa*. Hayashi gave no reasons for naming his specimen *frianti* rather than *tumulosa*. Intermarginal series of plates are also developed in the type material of *N. sphenisci*.

It should be noted that *Nardoa frianti* and *Gomophia egyptiaca* are sympatric for at least part of their ranges ; both have been taken in the Andaman Islands (Koehler), on Macclesfield Bank and in the Loyalty Islands. Koehler gave insufficient information about his material of *Gomophia* from the Andamans for me to be certain whether it should be left in *egyptiaca* or referred to subspecies *egeriae,* though his photograph suggests that the aboral skeleton is fairly open giving a reticulate appearance and thus linking it with *egyptiaca* sensu stricto. Following from the variation in shape of the abactinal tubercular plates in *G. egyptiaca egeriae,* I cannot help suspecting that Koehler's unfigured syntype (or paratype) of *N. frianti* should have been referred to *Gomophia.* This would account for the discrepancies between his description and the Macclesfield Bank specimens which I have referred to *frianti* with regard to the occasional presence of intermarginal plates and the absence of actinal papulae (though the latter could well evade detection if they are few in number).

The generic status of *Gomophia* is therefore in some doubt but, since the range of variation and specific limits of most of the species involved in the comparison have yet to be properly determined, I hesitate at present to refer it yet again to the synonymy of *Nardoa.* [In this it must be confessed that I am influenced to some extent by respect for Gray's eye for a genus, so often vindicated].

Included in the table is a column dealing with the shape of the arm tips, whether blunt or attenuated. However, since several of the species of *Nardoa* appear to be particularly susceptible to loss of parts of the arms, the subsequent regeneration, when incomplete, may give a false impression of the true shape. However, the mutilated holotype of **Nardoa mamillifera** Livingstone has all three of there maining arms ending abruptly, R/r being 5·7/1. Similarly abbreviated arms are found throughout in the two specimens I have seen from the Loyalty Islands (R/r 5·7/1 and 5·5/1), which otherwise agree closely with the three of *N. frianti* from Macclesfield Bank. The latter all have markedly attenuated arms with R/r 7·75–8·2/1. In the syntypes of *N. frianti* the ratio is 7·3 and 7·1/1, while Domantay and Roxas (1938) recorded a specimen from the Philippines with a value as high as 8/1. Döderlein (1926) recorded as *N. frianti* one from the Caroline Islands with R/r 6·4/1 but Hayashi (1938) identified as *N. tumulosa* his tuberculated Carolinian specimen; this has relatively short though tapering arms, R/r being only 5/1. A specimen from the Ryu Kyu Islands which Hayashi (1938*a*) similarly named *tumulosa* has R/r 5·3/1. In Fisher's holotype of *N. tumulosa* the ratio is 6·4/1. There is considerable resemblance between the Ryu Kyu specimen and the individual taken by the Barrier Reef Expedition which Livingstone (1932) referred to **Nardoa rosea.** Despite Livingstone's assurance that the latter agrees perfectly with the original description of *rosea* and shows no variation, a direct comparison with a paratype of *N. rosea* (Pl. 5, figs. 3 and 4) reveals a marked disparity in the size and convexity of the larger abactinal plates, many of which in the Barrier Reef specimen are c. 3 mm. in transverse diameter and c. 1·5 mm. in height (compared with c. 2 mm. and <1 mm. in *rosea*) so that it is far more reminiscent of the holotype of *N. mamillifera,* described by Livingstone in 1930, though the height of the convex plates is less. In addition it has some resemblance to the holotype of *N. gomophia,* not only in the dimensions of the plates but also in the spaced granulation and fairly attenuated arms, R/r being c. 7·5/1. The character of the alternating enlarged supero-marginals which H. L. Clark thought to be characteristic of *N. rosea* is shared by several other nominal species, notably by *N. frianti, gomophia, sphenisci* and possibly by the holotype of *N. mamillifera*, judging from what can be seen in the photographs of the last-named. However, Fisher mentions no alternation in the holotype of *N. tumulosa*. I doubt whether the number and shape of the abactinal tubercles are much use for the specific distinction of *tumulosa* as these seem rather variable in the material from Macclesfield Bank ; possibly both *mamillifera* and *tumulosa* will prove to be conspecific with *N. frianti*, though if a consistently blunt-armed species exists at the Loyalty Islands and off Queensland this could be distinguished as *mamillifera*.

As for **Nardoa gomophia,** the distinct though isolated abactinal tubercles are intermediate in size and shape between those of **Nardoa tuberculata** and *N. frianti*. Whereas *tuberculata* (Pl. 4, figs. 1–3) has relatively low and infrequent tubercular plates, often restricted to the sides of the distal parts of the arms and rarely exceeding 2·5 mm. in diameter or over 1 mm. in height, *N. gomophia* has tubercles on the disc, arm bases and midradial as well as lateral parts of the arms throughout their length, in size up to almost 3 mm. diameter and with height often exceeding 2 mm. The modification of the supero-marginal plates is also intermediate in *gomophia*, the first five to ten plates in each series and then every second plate, with almost complete regularity, being distinctly convex and projecting c. 0·5 mm. so as to give a slightly scalloped outline to the body. The alternate supero-marginals are markedly reduced in size and convexity, as in *N. rosea*. In *N. tuberculata* the supero-marginals are all similar and barely convex but in *N. frianti* a number of them are more convex, well over 1 mm. high and there is a tendency for alternate plates to be so modified.

The slender attenuated form of the arms of *N. gomophia* (R/r being 7·7/1) also distinguish it from *N. tuberculata*, nine specimens of which (including the holotype) have an R/r range of 5·2–6·8/1 with a mean of 6·0/1, the arms of all of them having blunt tips. Concurrently with the blunt-tipped arms, the main series of actinal plates in *N. tuberculata* runs for almost the entire arm length, whereas in specimens with attenuated arms, such as the holotype of *N. gomophia* and the Macclesfield Bank specimens of *N. frianti*, the adambulacrals and infero-marginals are in direct contact for at least the last quarter of the arm length. At least one of the two blunt-tipped specimens of *frianti* from the Loyalty Islands has the series of actinal plates extending for more than three-quarters of the arm length.

The structure of the aboral skeleton in *N. gomophia* is very similar to that of the holotype of *N. tumulosa*. However, the much greater extent of the actinal plates, the alternating form of the supero-marginals, the complete absence of intermarginal plates and the presence of actinal papulae, though only about two per area, in *N. gomophia* seem to distinguish them.

Much closer to *N. tuberculata* comes the holotype of **Nardoa obtusa** (Pl. 4, figs. 2 and 3) which Fisher examined in 1914, concluding (1919 : 379) that " its relationship is with the strongly tuberculate forms, such as *frianti* and *tumulosa* " also (p. 385) he suggested that *obtusa* is a young *tuberculata* with " the tubercles a little more prominent than usual ". Like Hayashi (1938*a*) I fully agree with the latter conclusion. There is some resemblance to the holotype of *N. gomophia*, but the fact that the supero-marginals show no tendency for alternation in size, the actinal plates already extend for well over half the arm length and the arm tips are blunt (possibly correlated with the relatively small size of the specimen, R/r being 35/7·5 mm. = 4·7/1) all point towards synonymy with *N. tuberculata*. Hayashi treated *obtusa* as a forma of *tuberculata* with relatively shorter arms and some colour difference in life from *tuberculata* sensu stricto.

There is in the collections a specimen from Batjan, Moluccas (Pl. 4, fig. 4) which I can only designate " *Nardoa* sp. aff. *tuberculata* ". Although registered in 1949, it is much older, carrying labels first as *Linckia tuberculata*, then *Ophidiaster tuberculata* (possibly in Bell's hand) and finally *Nardoa tuberculata* (printed for exhibition). The arms are much more slender than is usual in *tuberculata* and the tubercles more prominent and numerous but the compact aboral skeleton, the un-modified supero-marginal plates and the extension of the actinal plates right to the arm tips all agree with *N. tuberculata*. Von Martens (1866) commented on similar slender-armed specimens from Batjan.

Turning to **Nardoa sphenisci** nov., this species certainly approaches *Gomophia egyptiaca*. Two of the seven specimens from Macclesfield Bank which I am describing as subspecies *egeriae* of *G. egyptiaca* have most of the elevated abactinal and supero-marginal plates unusually rounded at the apex, though a few are more conical in shape, and there are several enlarged granules rather than a conical tubercle at the apex. Consequently the individual tubercular plates of these particular specimens are very reminiscent of those found in *N. sphenisci*. However, not only do these plates reach a much greater height in *Gomophia*, many of them being c. 2·5 mm. high, (when R is 60–65 mm.) but also they contrast markedly with the almost flat surrounding plates from which they arise in isolation. The granulation of the low plates is almost uniformly fine and, in general, even near the apices of the convex plates, the granulation is much finer in *G. egyptiaca* than in *N. sphenisci*, the granules on the flatter parts of the plates numbering 60–110/sq. mm. where counted in the former and only c. 30/sq. mm. in *sphenisci*. The development of intermarginal plates is another point of resemblance between the two species but the absence of pore areas on the lower surface below the infero-marginals and the lesser extent of the actinal plates (rarely to half R) in *G. egyptiaca* are in marked contrast. Also the armament of the adambulacral plates is rather different ; in *Gomophia* the two rows of spines usually project abruptly from the fine granulation of the lower side with no transitional enlarged granules forming a third series, whereas in most species of *Nardoa*, including *sphenisci*, the transition is more gradual. *G. egyptiaca* too may have five slender furrow spines, even at R c. 65 mm., though the number is more often four.

Finally there is some resemblance, geographically as well as morphologically, between *N. sphenisci* and *N. rosea*, both being known from northern Australia. In his key, H. L. Clark included *rosea* among the species of *Nardoa* lacking abruptly enlarged and projecting abactinal plates but his photograph of the holotype shows that some of the plates, especially the proximal midradial ones, are distinctly convex, approximating to the form of the corresponding plates of *N. sphenisci*. The rugose texture produced by the coarse granulation is another point of similarity and I was inclined to refer the " Penguin " specimens to *N. rosea*. Thanks to Dr. H. B. Fell and Mr. James F. Clark I have been able to study type material of *N. rosea* from the Museum of Comparative Zoology for comparison. This does have a considerable resemblance in the aboral skeleton to *N. sphenisci* though the size and convexity of the larger plates is rather less, their diameter not exceeding 2·0 mm. while few of them reach a height of 1·0 mm. The denuded skeleton is similarly compact though there is not so much size discrepancy between large and small plates. The resemblance in granulation, however, proved to be more superficial, since all the granules in *N. rosea* are more or less widely spaced from each other, as in the holotype of *N. gomophia*, not forming the almost continuous coating found in *N. sphenisci*. Also the granules are simply rounded, not flat-topped, although some of the larger ones on the convexities of the plates are slightly polygonal in outline. The number of fine granules interstitially is similarly c. 25–30/sq. mm. and of coarse ones 10–12/sq. mm. in *N. rosea* but, being spaced, the size of the individual granules is less than in *sphenisci*. Another difference lies in the adambulacral spines, the two rows of which in *N. rosea* stand out abruptly, whereas in *sphenisci* there is a transitional third row of elongated granules.

More obvious differences lie in the blunt-tipped rather than attenuated arms of *N. rosea* and the complete absence of intermarginal plates despite the strong tendency in both for alternation in size of the supero-marginals. Mr. Clark found no intermarginals in the rest of the type material in the Museum of Comparative Zoology, which he kindly examined for me. He gives the R/r ratios as 6·9/1 (in the holotype), 7·5/1, 7·3/1 and 6·8/1. In the paratype lent to me R is c. 78 mm. and the arm breadth at the very tip is as much as 4·5 mm., compared with c. 2 mm. in the holotype of *N. sphenisci*.

There is a specimen in the British Museum collections from Bassett-Smith Bank (also off northern Australia) which I had identified as *N. rosea* some years ago. It is in spirit, which may partly account for the smoother appearance in comparison with the type material of *rosea*, but the granules are almost continuous, not spaced from each other, though they are similar in number. However, alternate supero-marginals, especially distally, are regularly reduced in size. R/r is 7·0/1. The proximal midradial abactinal plates are only slightly convex and are relatively larger than in the type material of *N. rosea* with five plates rather than about seven across the base of the arm. There is no sign of intermarginal plates. This specimen is certainly not conspecific with Livingstone's one from the Barrier Reef and possibly not with the type material of *N. rosea* either. Obviously much still remains to be ascertained about the specific limits of these species.

In view of the intermediate condition of the aboral skeleton shown by *N. rosea* and the close affinity between *N. tuberculata* and *pauciforis* discussed further below, the division of the species of *Nardoa* into two groups according to the occurrence of distinctly convex plates is not a sharp one. Nevertheless it is a convenient distinction for most of the species.

The remaining species of *Nardoa*—those with all the abactinal plates of similar low or flat contour—include the following :

Nardoa variolata (Retzius), 1805—the type-species
Nardoa lemonnieri Koehler, 1910

Nardoa mollis de Loriol, 1891
Nardoa novaecaledoniae (Perrier), 1875
Nardoa galatheae (Lütken), 1865
Nardoa pauciforis (von Martens), 1866
Nardoa faouzii Macan, 1938 and
Nardoa rosea H. L. Clark, 1921—if that is not included in the first group.

The limits of **N. variolata** need re-examination. Bell has recorded the species from Stanley Gardiner's collections at various islands in the western Indian Ocean (1909) and from the Maldives (1902) as well as from Dr. Ondaatje's collections in Ceylon (1887). The last record was based on three small specimens (R up to 28 mm.) and I believe that these are conspecific with the much larger specimens from Ceylon which Bell referred to *N. novaecaledoniae* (Perrier) and which I am currently relabelling as *N. lemonnieri* Koehler, being unconvinced by H. L. Clark's proposal to synonymize the latter with *N. mollis* de Loriol. Nearly all the Gardiner specimens are in the Cambridge Museum. I have studied one of these from S. Nilandu, Maldives. This is not a *Nardoa* at all but is conspecific with another Gardiner specimen from the Amirantes, which is in the British Museum collections. I consider that both of them represent a new species of *Fromia* described below. I cannot say whether the specimens from the second Maldive locality of Gardiner's are really referable to *N. variolata*. H. L. Clark has already commented that the specimens from at least Minikoi recorded as *N. novaecaledoniae* by Bell must surely have been in reality *Linckia laevigata*, judging from their blue colour—the species of *Nardoa* being various shades of brown. However, in 1957, Major W. W. A. Phillips presented the British Museum with two specimens from Male in the Maldives which were referred to *N. variolata* (Clark & Davies, 1966) on the basis of H. L. Clark's key to the species of *Nardoa* (1921), since the largest abactinal plates exceed 3·0 mm. in transverse diameter, even 3·5 mm. in one specimen, and there is no abrupt reduction in size of the plates distally. One of the two has only four arms and R is 85 mm. The second, five-armed, specimen has R 95–105 mm. *N. variolata* at Mauritius and East Africa rarely exceeds R 70 mm., though the single specimen taken by the Transit of Venus Expedition at Rodriguez and named by Smith does have R 100–110 mm. The large size and the proportions of the abactinal plates of the Maldive specimens approximate to the figured syntype of **N. lemonnieri** from the Andaman Islands, though the arms are probably somewhat broader terminally. Unfortunately Koehler cut off all the arm tips from his photographs of *lemonnieri* in making up the plate ; as far as can be seen the arms are fairly slender distally ; he describes them as narrow and sharp at the tip. In his three larger specimens, R 95+ mm., R/r is 6·6, 7·0 and 8·0/1.

The British Museum collections include three large individuals of *N. lemonnieri* from the Andaman Islands, one with four arms being excluded from table 2, and eleven from Ceylon, three of them very small. As can be seen from the table, these all have relatively more attenuated arms than the two from the Maldives and their distal aboral plates are consistently smaller, though the diminution in size distally is similarly fairly gradual. The Maldive specimens therefore seem to be intermediate both morphologically and geographically between *Nardoa variolata* from the Mascarene Islands and East Africa and *N. lemonnieri* from Ceylon and the Andaman Islands but their true status must await the study of further material to show the extent of variation.

Some details of all these specimens together with data from available material of **N. mollis** and **novaecaledoniae** is given in table 2. Apart from the quoted types, all the specimens are in the British Museum collections except for five of *novaecaledoniae* from the type-locality, which are on loan from the Oslo Museum.

Were it not that Perrier gives R/r of the holotype of *N. novaecaledoniae* as 6·7/1, I would have thought from the present material that the species can be differentiated from *N. lemonnieri* and *mollis* by the moderate length of the arms and their lack of attenuated tips, as Koehler (1910) also remarked. However, H. L. Clark (1921) distinguished *novaecaledoniae* by the relatively larger proximal aboral plates, as well as by a colour difference of little use for the determination of preserved specimens. Unfortunately only two specimens of *N. mollis* are available to me. These do tend to substantiate the distinction from *novaecaledoniae* by the smaller size of the proximal aboral plates and the more attenuate arm tips.

Apart from the specimens shown in Table 2, there is one from Timor the identity of which with *N. lemonnieri* or *N. mollis* I am uncertain. It has R 115–125 mm., R/r 7·5/1, br 10 mm. from arm tip 5·0 mm., the arms being very attenuated, maximum aboral plate diameter just over 3 mm., distal plate diameter c. 0·8 mm. and seven to nine plates across the arm width basally. The distal plates are extremely elongated and the enlarged polygonal granules which they bear tend to be arranged in two rows of about five granules each. The interstitial areas between the groups of large granules are occupied by only about two rows of much finer ones. This contrasts on the one hand with the irregular-shaped groups each of about four large granules shown by de Loriol (1891, pl. 3, fig. 4*c*) on the distal plates of the holotype of *N. mollis* and on the other hand with the broader, though still somewhat elongated, groups of 12–18 granules found in the specimens of *N. lemonnieri* from the Andaman Islands, while the individuals from Ceylon have even larger distal plates.

Domantay and Roxas (1938) have recorded *N. variolata, mollis, novaecaledoniae* and *lemonnieri* all from the Philippines. Judging from their photographs the first-named is certainly not conspecific with the species found at Mauritius but is probably based on a specimen of *N. novaecaledoniae*; their other identifications may be correct. The individual named *N. lemonnieri* (Pl. 10, figs. 55, 56) has extremely attenuated arms and some resemblance to the British Museum specimen from Timor except that the proximal aboral plates are smaller. Fisher too (1919) has recorded as *N. lemonnieri* a specimen from the vicinity of the Philippines (the Sulu Archipelago) ; this has R/r 7/1 so that the arms are elongated if not attenuated.

The position of **Nardoa galatheae** (Lütken) also remains to be determined. The unique type was from the Nicobar Islands and the arms were described as narrow and acute, though R/r is only c. 6/1, so that there is a strong probability that its affinities lie with *N. lemonnieri*, which may also have four furrow spines.

In addition to the characters already discussed, Fisher has used the occurrence of an abrupt reduction in magnitude of the aboral granulation at the edges of the

TABLE 2.

Species	Locality	R (mm.)	R/r –/1	br 10 mm. from tip (mm.)	Diameter of aboral plates Max. (mm.)	distal (mm.)	No. pls. across arm base
N. variolata	Rodriguez	105	5·8	8·0	4·0	2·5	c. 9
	Mozambique	68	5·7	6·0	4·0	2·0	c. 7
	,,	67	5·6	7·5	3·5	2·0	c. 7
	Mauritius	67	5·3	8·5	4·5	2·5	5
	,,	66	5·6	7·5	4·5	2·5	5
	,,	63	4·8	7·5	3·5	2·0	4, 5
	,,	62	5·2	6·5	4·0	2·0	c. 7
	,,	62	5·6	5·5	2·5	1·5	c. 7
	,,	60	5·0	5·0	3·5	2·0	c. 5
	,,	58	5·7	6·0	4·0	2·0	5–7
	Zanzibar	58	4·8	7·0	4·0	2·0	c. 5
	Mauritius	57	4·7	6·0	3·5	2·0	c. 7
	,,	55	5·0	7·0	3·0	2·0	6, 7
R/r range of 12 with R 55–68 mm. = 4·7–5·7/1, mean 5·2/1							
Nardoa sp.	Maldive Is.	100	6·6	8·5	3·7	2·0	5, 6
	,,	85	6·5	7·0	3·3	2·0	c. 8
N. lemonnieri T*	Andaman Is.	98	7·0	?	3·5	1·5	c. 7
	,,	118	6·9	5·5	2·5	1·2	c. 9
	,,	115	6·6	5·0	2·5	1·0	7–9
	Ceylon	114	6·6	7·0	3·2	1·5	7, 8
	,,	110	7·4	6·0	3·2	1·7	c. 7
	,,	88	5·6	6·0	2·5	1·2	c. 7
	,,	85	6·0	5·5	2·5	1·5	c. 7
	,,	76	5·9	6·0	2·5	1·2	c. 7
	,,	72	6·2	5·5	1·7	1·2	c. 7
	,,	65	5·4	5·5	2·0	1·2	6, 7
	,,	57	5·7	6·0	2·0	1·2	c. 7
R/r range of 11 with R 57–118 mm. = 5·4–7·4/1, mean 6·4/1							
N. mollis T*	New Britain	111	7·0	5·5	2·5	c. 0·5	?
	Monte Bello Is.	90	6·4	5·0	2·0	0·7	c. 7
	,, ,, ,,	65	6·0	5·0	1·5	0·7	c. 7
N. novaecaledoniae T*	New Caledonia	94	6·7	—	3	—	c. 10
	,, ,,	95	5·6	7·0	3·0	1·0	7, 8
	,, ,,	92	5·4	7·5	3·0	0·7	c. 9
	,, ,,	85	5·8	7·5	3·0	0·7	7–9
	Barrier Reef	92	7·1	7·0	3·0	1·0	c. 9
	Fiji	84	5·3	8·0	2·5	0·8	7–9
	New Caledonia	75	5·8	7·5	3·0	1·0	c. 7
	,, ,,	75	5·5	6·5	2·5	0·8	c. 7
	,, ,,	72	5·2	5·5	2·5	1·0	7–9
	Port Essington	74	5·7	6·0	2·0	0·5	6, 7
	,, ,,	74	5·2	5·5	2·5	0·8	6, 7
	,, ,,	72	5·2	6·0	2·0	0·5	c. 7
	,, ,,	72	5·5	5·5	2·0	0·5	c. 7
	,, ,,	55	5·0	6·0	2·5	0·5	6, 7
	Duke of York I.	63	5·2	6·0	2·0	0·5	c. 7
R/r range of 13 with R 55–95 mm. = 5·0–5·8/1, mean 5·4/1							

TABLE 2. Data from specimens of four species of *Nardoa* for comparison with two from the Maldive Islands. The distal br measurements are given to illustrate the degree of attenuation of the arms. The diameters of the plates are approximate measurements made without denuding the plates. The entries for the relevant types (marked T*) are derived from the literature and the approximately life-sized figures given by Koehler and de Loriol.

plates and a lobate form of the denuded plates to try and distinguish between the species of *Nardoa*. H. L. Clark discounts the latter and I too have found lobate plates to be more widespread among the species of *Nardoa* than Fisher supposed. As for the granulation, this seems to be variable ; it can give a very distinctive appearance when the change to fine interstitial granulation is abrupt but this may be exaggerated to some extent by the state of preservation. Contrary to Fisher's statement, an abrupt change in size of the granules does occur in *N. novaecaledoniae* as well as in *N. variolata, lemonnieri* and *mollis*. However, it may be less marked in **Nardoa pauciforis,** which differs too from the other four species by regularly possessing pedicellariae of the split-granule kind among the interstitial granules but distinctly coarser than these. The abactinal plates are also particularly small in *N. pauciforis*, not even the proximal mid-radial ones approaching the marginal plates in size so that there are usually about 13 plates across the width of the arm basally when R is c. 100 mm.

Hayashi (1938) considers *Nardoa pauciforis* to be a forma of *N. tuberculata*, noting that it differs only in lacking the scattered tubercular aboral plates. The colouration of the two he says is similar as well as the other morphological characters. Certainly *N. tuberculata* has arms of similar shape, extensive actinal plates, granulation little finer interstitially than on the abactinal plates and interstitial pedicellariae usually present. However, the holotype of *N. tuberculata* with R 82 mm. has only nine or ten aboral plates across the width of the arm basally and other specimens in the British Museum collections with R c. 100 mm. rarely have more than eleven plates. Without larger samples for study I cannot comment further on this problem.

Finally **Nardoa faouzii** Macan differs from all the other species in the conspicuously regular arrangement both longitudinally and transversely of the abactinal plates of the proximal third or nearly half of each arm. This is comparable to the arrangement in *Scytaster semiregularis* Müller and Troschel, which was for long included in *Nardoa* but split off by H. L. Clark as type-species of the genus *Certonardoa*, though Tortonese (1955) does not approve this action. *Certonardoa* is distinguished from *Nardoa* not only by the skeletal arrangement but also by the complete absence of papulae below the infero-marginal plates, whereas *N. faouzii* does have well-developed actinal series of pore-areas, numbering 14 or 15 on each side of each arm. H. L. Clark also referred to *Certonardoa* two species described by Koehler (1910), *Nardoa carinata* from the Andaman Islands and *N. squamulosa* from Burma. I am uncertain about the affinities of the latter. However, there is a specimen with R 42 mm. from south of Galle, Ceylon, collected by Dr. Herdman, in the British Museum. It is similar to the holotype of *C. carinata* not only in size but also in the semi-regular arrangement of the aboral skeleton, the tapering arms almost flat below (though rounded rather than slightly carinate above) and the absence of inter-marginal or actinal papulae. However, the Sinhalese specimen has a number of well-developed alveolar pedicellariae on the larger plates. Probably on this account, coupled with the partially regular abactinal plates, it was formerly labelled as an *Ophidiaster* or *Tamaria* but the more Goniasterid-like adambulacral armament serves to distinguish it from these genera. In comparison with this specimen, *N. faouzii* has blunt arms, no pedicellariae and pore-areas present not only inter-marginally but also below the infero-marginals in an extensive series.

The partially regular arrangement of the skeleton is I believe a character of some weight, distinguishing *faouzii* easily from *N. variolata* and all the other species discussed above. However, since it is not supported by a difference in the extent of the pore-areas, I consider that the distinction should be only at the subgeneric level. Accordingly I propose to establish the following :—

NARDOA subgen. ***ANDORA**** nov.

Type species. *Nardoa faouzii* Macan, 1938.

Diagnosis. A subgenus of *Nardoa* with the aboral plates of the proximal third of the arms arranged in regular longitudinal and transverse rows.

Key to the Species of *NARDOA*

1 A number of isolated abactinal plates abruptly more convex and projecting than the rest, often hemispherical 2

1′ Abactinal plates mostly similar in contour, though often variable in size, none markedly projecting 6

2 Some of the supero-marginal plates hemispherical as well as some abactinal plates, the height of these often equal to the basal diameter[1] . ***frianti*** Koehler, 1910
mamillifera Livingstone, 1930

2′ No supero-marginal plates conspicuously tubercular, though in some species the alternate ones may be more or less convex ; tubercular abactinal plates distinctly wider than high, though sometimes no broader than the unspecialized flatter plates 3

3 Tubercular abactinal plates low, broad and cushion-like, absent from the distal parts of the arms, often transversely elliptical, measuring 3–4 mm. in diameter at $R > 50$ mm. . . . . ***tumulosa*** Fisher, 1917

3′ Tubercular plates relatively small, rarely much exceeding 2 mm. in diameter, even at $R > 70$ mm., often present distally as well as (or rather than) proximally . 4

4 Arms not attenuated but more or less blunt at the tip, R/r 5·0–7·0/1 ; the main actinal row of plates extending the whole length of the arm ; tubercular abactinal plates inconspicuous, tending to be fewer proximally and restricted to the lateral areas of the distal parts of the arms ; supero-marginal plates all similar in size, not alternating . . . . ***tuberculata*** Gray, 1840

4′ Arms very attenuated distally, R/r 7·5–9·2/1 (in the only four specimens known) ; the main actinal row of plates terminating at half to two-thirds R from the base of the arm ; tubercular abactinal plates well-developed, proximally as well as distally ; some of the supero-marginals, often alternate ones, reduced in size . 5

5 Intermarginal plates present in the arm angles ; the majority of abactinal plates markedly convex, particularly the midradial ones . . . ***spheniscі*** sp. nov.

5′ No intermarginal plates ; tubercular abactinal plates widely separated, as well-developed laterally as mid-radially . . . ***gomophia*** (Perrier), 1875

6 Supero-marginal plates tending to alternate large and small, especially distally
rosea H. L. Clark, 1921

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* An anagram of Nardoa.

[1] If the abruptly terminating arms of the mutilated holotype of *N. mamillifera* are shared by other specimens from the type-locality this might provide a valid distinction from *N. frianti*, in which case specimens from the Loyalty Islands could also be referred to *mamillifera*.

6′ No regular alternation in size of the supero-marginals 7

7 Abactinal plates of the proximal third to half of the arm forming distinct regular longitudinal and transverse series, though this breaks down distally **Nardoa (Andora) fouazii** Macan, 1938

7′ Abactinal plates irregular in arrangement throughout 8

8 Adambulacral plates each bearing only four furrow spines and four subambulacral ones (though in my interpretation of Lütken's danish the granulation backing on to these spines is transitional) . . . . . . **galatheae** (Lütken), 1865

8′ Granulation of the outer part of each adambulacral plate usually modified to form a third row of spines, numbering three like the two inner rows, though the furrow series may consist of four spines 9

9 Many of the abactinal plates more or less conspicuously broadened and alternating to form an almost continuous pavement, the interstitial pore-areas being small ; the larger plates markedly bigger than the supero-marginals, exceeding 3 mm. in diameter, even at R only c. 40 mm., numbering only about five across the width of the arm basally at R < 50 mm., seven at R 50–70 mm. or up to nine in the rare specimens that exceed 70 mm. ; the distal abactinal plates similar to the proximal ones though gradually becoming smaller . . **variolata** (Retzius), 1805

9′ Few if any of the abactinal plates conspicuously larger than the supero-marginals and rarely broadened transversely to exceed 2·5 mm. in diameter ; if some large plates are present proximally then the distal plates are relatively much smaller, often with an abrupt change in magnitude at about two-thirds R . . . 10

10 All the abactinal plates, both proximally and distally, small in comparison with the marginal plates, numbering about 13 across the arm width basally, at least at R > 90 mm. ; granuliform pedicellariae often present between the aboral plates and distinctly coarser than the granules ; ventral papulae few and inconspicuous **pauciforis** (von Martens), 1866

10′ The proximal abactinal plates, especially midradially, distinctly larger than the distal plates and sometimes equalling or even slightly exceeding the supero-marginals in diameter, rarely more than eleven plates across the width, more often seven or nine ; pedicellariae not recorded ; usually a number of pore-areas developed between infero-marginal and actinal plates 11

11 R/r usually 5·0–6·0/1 (see Table 2) . . **novaecaledoniae** (Perrier), 1875

11′ Arms more attenuated, R/r usually 5·5–8·5/1 12

12 Distal abactinal plates conspicuously smaller than the proximal ones, not exceeding 1 mm. in transverse diameter, their positions shown by rounded groups of coarse granules among the fine interstitial granulation . . **mollis** de Loriol, 1891

12′ Distal abactinal plates becoming gradually somewhat smaller than the proximal ones and usually 1·2–1·5 mm. in diameter but markedly elongated in form with ovate groups of coarse granules . . . . . **lemonnieri** Koehler, 1910

Fromia indica (Perrier)

Scytaster indicus Perrier, 1869 : 255 (?63).

Fromia indica : Perrier, 1875 : 177–178 (441–442) ; Koehler, 1910 : 140, pl. xvii, figs. 7, 8 ; H. L. Clark, 1921 : 42 ; Hayashi, 1938*a* : 207 ; 1938*b* : 59–62, figs. 1, 2, pl. iv, figs. 1–4 ; 1938*c* : 279–280.

Fromia tumida Bell, 1882*a* : 124, pl. vi, fig. 4 ; H. L. Clark, 1921 : 41.

Fromia andamanensis Koehler, 1909 : 105–108, pl. vii, figs. 5, 6 ; H. L. Clark, 1921 : 41.

Fromia elegans : Engel, 1938 : 11, fig. 1, pl. iii, fig. 1 [Non *F. elegans* H. L. Clark, 1921].

Fromia indica forma *andamanensis ;* Hayashi, 1938 : 428–430, pl. ii, figs. 7, 8.

MATERIAL. Ceylon ; Mr. Kelaart ; two syntypes of *Fromia tumida* Bell, B.M. reg. no. 52.5.15.62 and 63.

Ceylon ; Dr. Ondaatje ; 1 specimen, no. 88.4.13.3.

Andaman Islands ; Dr. Anderson ; 5 specimens, no. 86.6.26.20–22 and 79.

Fiji Islands ; Admiralty ; 1 specimen, no. 56.9.24.26.

SYNONYMY. I agree with Hayashi (1938 and 1938*b*) that *Fromia andamanensis* Koehler is better ranked as no more than a forma of *F. indica* distinguished by the similar dimensions of the abactinal plates as opposed to forma *indica* with two series of enlarged plates along each arm. The material in the British Museum collections from the type-locality of *andamanensis* supports this synonymy. However, I do not agree that *F. elegans* is also a synonym, since Mr. James F. Clark has re-examined the holotype in the Museum of Comparative Zoology at my request and found that the granules of the actinal plates number seven to nine on a plate and are no higher than wide, differing from the very characteristic elongated granules or short blunt spines, usually in groups of about five, found in *F. indica*. My thanks are due to Mr. Clark for his observations. Both Domantay and Roxas (1938) and A. H. Clark (1949) have extended the geographical range of *F. elegans* from Torres Strait to the Philippines. Judging from the photographs given by the former, their specimens could well be *elegans* but the specimen from Banda Neira referred to *elegans* by Engel (1938) has the distinctive elongated armament of the actinal plates characteristic of *F. indica*.

To the synonymy of *F. indica* must also be added *Fromia tumida* Bell. The syntypes are dried and have suffered some distortion so that the lower surface has become concave and the arms are probably unnaturally wide. The hollowed under side probably evoked Bell's erroneous statement that the adambulacral spines are smaller than the spines of the actinal plates. In fact the armament is just like that of *F. indica* with short spines on the actinal plates and slightly longer ones on the adambulacrals.

Fromia nodosa sp. nov.

(Pl. 6, figs. 1–3)

Ferdina Offreti (pt.) Koehler, 1910 : 143, 147, pl. xvi, figs. 4, 5 only.

MATERIAL. Amirante Islands, W. Indian Ocean ; Gardiner collection ; the holotype and one paratype. B.M. reg. no. 1907.7.1.95 and 96.

South Nilandu, Maldive Islands ; Gardiner collection ; 1 specimen. Cambridge Museum.

DIAGNOSIS. A species of *Fromia* with very conspicuous alternation in size and shape of the supero-marginal plates, the larger ones being abruptly convex and separated by less than their own width from the series of similarly enlarged and convex spaced carinal plates ; no crystal-bodies embedded in the surface of the plates.

DESCRIPTION OF THE HOLOTYPE. R/r = 32 mm./7·5 mm. = 4·3/1 ; br at base 7·5 mm. and at arm tip 3·5 mm. The body is flattened above and the arms taper evenly to blunt tips.

The abactinal plates are of two distinct kinds, the majority being flat and polygonal while nine to eleven spaced carinal plates on each arm, starting with the primary radial plates, are enlarged, up to 2·75 mm. in transverse diameter (slightly less longitudinally), rounded in outline and markedly convex, standing out sharply from the surface though not exceeding 1 mm. in height. When denuded, the plates between the convex carinal ones are revealed as not part of the series, some being adradial in position though others may be midradial. All the plates are slightly notched at intervals peripherally to accommodate the single interstitial papular pores. There are four to six pores around each of the flatter plates but seven to nine round most of the enlarged ones. The surface of the denuded plates is almost smooth, there being no embedded crystal-bodies.

The supero-marginals are similarly of two forms with almost perfect alternation, the larger ones equal to or even slightly exceeding the diameter of the enlarged carinal plates. The swollen supero-marginals alternate in position obliquely with the swollen carinals, the three series on each arm being separated by only single small flat plates for most of the arm length while from the tenth supero-marginal all three rows of swollen plates are partially in contact laterally or obliquely. There are fifteen supero-marginal plates in one series denuded, the first, second, fourth, sixth, eighth, tenth, twelfth, fourteenth and fifteenth being convex and dwarfing the intervening plates.

The infero-marginals number sixteen and are all similar in form though gradually decreasing in size from a proximal breadth of c. 2 mm.

There are two series of actinal plates, the outer consisting of ten plates and extending to the fifth infero-marginal, two actinal plates corresponding almost exactly to one marginal. The inner row consists of 24 plates (in the series denuded) extending to the middle of the eleventh infero-marginal or 25 mm. distance from the mouth.

All these plates are covered with a continuous coat of polygonal granules which are slightly larger on the swollen abactinal and supero-marginal plates, numbering c. 35/sq. mm. as opposed to c. 55/sq. mm. on the flatter plates. Adjoining many of the papular pores one or sometimes several of the granules are distinctly enlarged.

There are about 46 adambulacral plates in each series. Four or five of the basal ones bear four furrow spines, the adoral one of these usually smaller and inset on the plate, like a thumb. The remaining plates, except at the very tip of the arm, each have three furrow spines. These are flattened and spatulate, measuring up to 0·75 mm. in length. Separated from the furrow spines by a distinct gap come two subambulacral spines, which are about two-thirds as long as the furrow spines but slightly stouter. Between the twenty-fifth and thirtieth adambulacral plates the number of subambulacral spines falls to one. The outer part of each plate is covered with small low polygonal granules similar to those on the actinal plates and abruptly contrasting with the projecting subambulacral spines.

There are two series of single actinal papulae corresponding in extent to the actinal plates.

PARATYPES. The second specimen from the Amirantes has R/r = 19 mm./5 mm. = 3·8/1 and closely resembles the holotype except that the arms maintain the same width for about two-thirds of their length. Also the enlarged supero-marginal plates are distinctly bigger than the enlarged carinals. The second series of actinal plates consists of only one or two plates. There are only about five actinal papulae between the proximal infero-marginals and the main series of actinal plates.

The Maldive specimen (Pl. 6, fig. 3) has R/r 34 mm./8·5 mm. = 4·0/1 ; br is 9·5 mm. basally but only 2·5 mm. at the tip, the arms tapering markedly. The swollen carinal and supero-marginal plates, particularly the latter, are even larger than in the holotype, producing a very mosaic-like effect, the low interstitial plates occupying little area. The largest supero-marginals are as much as 4·0 mm. in breadth and 4·5 mm. in length. Again there is a distinct enlargement of one or more granules near many of the papular pores and there are two rows of actinal papulae ; in one infero-marginal series there are 17 plates.

REMARKS. The specimen with R 13·5 mm. from Ceylon thought by Koehler (1910) to be the immature fully granule-covered form of his *Ferdina offreti* is probably referable to *Fromia nodosa*. The holotype of *Ferdina offreti* (R 37–38 mm.) from the Andaman Islands likewise has enlarged swollen supero-marginal and carinal plates but these are completely bare and contrast conspicuously in colour with the granular areas. Livingstone (1931) has since referred *offreti* to *Neoferdina*, which he characterized by the presence of some bare enlarged aboral and marginal plates, as opposed to *Ferdina* sensu stricto with complete granulation even though some of the plates may be convex. *Ferdina heffernani* Livingstone (referred below to a new genus) has a superficial resemblance to *Fromia nodosa* but differs in the single row of adambulacral spines and the absence of papulae from the under side. Since these two features also apply to *Ferdina* I have no doubt that *nodosa* is most appropriately placed in *Fromia*. Nevertheless it does provide an interesting link between these genera.

Only two other species of *Fromia* agree with *F. nodosa* in having a tendency for alternation in size and more or less marked convexity of the supero-marginal plates, namely *Fromia monilis* Perrier and *F. ghardaqana* Mortensen. The latter particularly may also have some slightly convex carinal plates but nowhere does the size and degree of projection of these enlarged plates approach the condition found in *F. nodosa* where these plates are separated laterally from each other by less than their own width, while in the distal third of the arm they are partially in contact with each other.

In *Fromia nodosa* too the surface of the denuded plates is almost smooth, whereas in the other two species there are numerous glassy knobs or crystal-bodies embedded in them. Among the other species of *Fromia*, crystal-bodies are present in *F. milleporella*, *armata* and *balansae* but absent in *indica* and *elegans* ; their occurrence in *F. hemiopla*, *hadracantha* and *pacifica* is unknown.

FERDINA Gray

Ferdina Gray, 1840 : 282 ; 1866 : 12–13 ; Fisher, 1919 : 370 ; H. L. Clark, 1921 : 58 ; Livingstone, 1931 : 305.

TYPE SPECIES. *Ferdina flavescens* Gray, 1840 ; designated by Fisher, 1919.

REMARKS. In 1931 Livingstone restricted *Ferdina* by splitting off *F. cumingi* Gray and several other species with some conspicuously naked plates as a new genus *Neoferdina*. At the same time he re-diagnosed *Ferdina* itself and added a new species, *Ferdina heffernani*. Unfortunately his generic diagnosis appears to have been based more on the latter than on the type-species, which he knew only from photographs of the holotype and the very inadequate published descriptions. Re-examination of the holotype of *F. flavescens* (Pl. 6, fig. 6) and the removal of the aboral granulation of one arm reveals that the skeleton is of similar form to that of *Gomophia* and some species of *Nardoa*, with larger abactinal plates placed at irregular intervals and superimposed on a reticulum of smaller plates leaving meshes of sufficient size to accommodate small groups of slightly spaced papulae. Probably because the specimen has R only 26–28 mm. the number of pores in each area is small, mostly two to four, which may form linear series around the larger plates so that the grouping is not obvious. Nevertheless, some grouping can be seen even with the granulation intact, this showing up both in the photographs of the holotype published by Livingstone and in de Loriol's drawings of a specimen from Mauritius, the type-locality. This is nothing like the condition in *F. heffernani*, which resembles *Fromia* in its polygonal close-fitting pavement of abactinal plates with isolated papulae at the angles.

In addition, in *flavescens* the supero-marginals are indistinguishable from the abactinal plates on the one arm cleared, only a few large ones near the arm tip being arranged in a linear series. This may also be the case in some larger specimens of *Gomophia egyptiaca* where the degree of specialization of the supero-marginals is variable.

Another unusual feature of *Ferdina flavescens* is that the actinal and adambulacral plates are embedded in tissue so that the uniform granulation covering them is almost completely smooth and conceals the limits of the underlying plates. In *F. heffernani* these plates are much more easily dislodged when the skin is dissolved by bleach and their presence is evident without denuding due to their contours and to the coarsening of the granulation in the middle of each one.

Finally, the armament of the adambulacral plates differs from that of *F. heffernani* in that the even granulation of the lower surface runs up the outer side of the single row of furrow spines, having shrunk in drying, leaving only the tips of the spines projecting. This produces somewhat the same effect as found in *Linckia* where the furrow spines appear to be sunk into the furrow. However, in *Linckia* the tips of the furrow spines hardly project at all from the surface. Possibly the same will prove to be true of live and spirit specimens of *Ferdina flavescens*, as opposed to dried ones.

Thus, although *F. flavescens* appears to agree with *heffernani* in having complete granulation, no actinal papulae and only a single series of adambulacral spines, in fact the two species are not at all closely related and are certainly not congeneric. It remains then to re-diagnose *Ferdina* and to establish a new genus to accommodate *F. heffernani*.

DIAGNOSIS. A genus of Ophidiasteridae with the aboral skeleton consisting of irregularly-placed larger plates superimposed on a reticulum of smaller ones leaving space between for small papular areas with poorly-integrated groups of usually two to four pores in each ; the limits of the underlying plates concealed by continuous even granulation ; supero-marginal plates irregular and only distinguishable from the abactinal plates near the tips of the arms ; actinal and adambulacral plates embedded in soft tissue so that their limits are concealed by the uniform granulation covering them ; no actinal papulae ; adambulacral plates armed with only a single row of short blunt furrow spines, only the outer halves of which project from the continuous granulation of the under side.

AFFINITIES. *Ferdina* thus becomes a monotypic genus. It seems to occupy an isolated position within the family but may have some affinity with *Gomophia*.

CELERINA gen. nov.

TYPE-SPECIES. *Ferdina heffernanii* Livingstone, 1931.

DIAGNOSIS. A genus of Ophidiasteridae with polygonal aboral plates, irregular in size, convexity and arrangement, having isolated papulae at the angles between ; supero-marginal plates tending to alternate large and convex with small and flat ; actinal plates not embedded in tissue ; granulation continuous all over, coarser on the centres of the actinal plates ; no actinal papulae ; a single row of short but projecting furrow spines.

Celerina heffernani (Livingstone)

(Pl. 6, figs. 4 and 5)

Ferdina heffernanii Livingstone, 1931 : 306–307, pl. xxiv, figs. 1–5.

MATERIAL. Macclesfield Bank, South China Sea ; 40–55 metres ; Admiralty ; 1 specimen, B.M. reg. no. 93.8.25.90.

This specimen was named *Fromia milleporella* by Bell.

DESCRIPTION. R/r = 29 mm./6 mm. = 4·8/1 ; br basally = 6·5 mm. The abactinal plates are mostly about 1·0 mm. in diameter and are irregular in arrangement, even the carinal series being indistinct proximally, though four to seven spaced carinal plates in the distal half of each arm are enlarged up to c. 1·5 mm. diameter and are slightly convex. At the base of the arm there are three or four plates across the width. The supero-marginal plates number about 17 in each series and exhibit a fairly regular alternation of large convex plates, up to 2·0 mm. in breadth and 2·4 mm. in length, with small flat plates in between. Consequently, the upper side superficially has considerable resemblance to that of *Fromia monilis*. The whole aboral surface is covered with a close coat of very fine granules, c. 150/sq. mm. These are very slightly coarser on the convexities of the skeleton but much less so than in the holotype of *F. heffernani*. However, on the distal marginal plates, especially the infero-marginal ones, the granulation is distinctly coarser centrally. There are about 19 similar infero-marginals in each series, decreasing gradually in size distally. In each arm angle there are about six narrow intermarginal plates, three each side of the inter-radius. The main series of actinal plates numbers about 20 with an odd inter-radial plate adjoining each pair of oral plates. The granulation of these is distinctly coarser than the aboral granulation and in the centre of each actinal plate one to four granules are both broader and higher than the rest. Similarly the adambulacral plates, after the basal three or four, have one or more enlarged granules in the centre, a single one on the distal plates becoming increasingly prominent though without reaching the eminence of a spine. Along the furrow margin runs a single series of small sharply-pointed spines up to 0·6 mm. long. On the first 15–18 plates these usually number three; the following plates normally bear two furrow spines. There are single papular pores between the angles of the abactinal plates and intermarginally but none on the lower surface.

REMARKS. The holotype of *Ferdina heffernani* from the Santa Cruz Islands (east of the Solomons) has R 40 mm., which may account for its more numerous enlarged abactinal plates and the coarser granules on the centres of these; however, Livingstone counted only two furrow spines, despite the larger size. He made no mention of intermarginal plates but these could easily be overlooked if they are as inconspicuous as in the British Museum specimen.

Tamaria tumescens (Koehler)

Linckia megaloplax (pt.) Bell, 1894 : 395.
Ophidiaster tumescens Koehler, 1910*a* : 281–283, pl. xvi, figs. 3, 4.
Tamaria tumescens : H. L. Clark, 1921 : 94 ; 1938 : 141 ; 1946 : 123–124.
Tamaria propetumescens Livingstone, 1932*a* : 369–371, fig. 1, pl. xlii, figs. 1–5.
Tamaria ajax Livingstone, 1932*a* : 371–372, fig. 2, pl. xli, figs. 1–5.

MATERIAL. Parry Shoal, Arafura Sea; 22 metres; Admiralty; 4 specimens including the holotype of *T. propetumescens* Livingstone, B.M. reg. no. 92.4.4.2–5. 1 specimen, no. 92.4.4.27.

Holothuria Bank, northern Australia; 27 metres; Admiralty; 1 specimen, no. 91.8.26.83. 2 specimens, no. 92.1.14.326–327.

Broome, N.W. Australia; presented by Museum of Comparative Zoology, Harvard; 1 specimen, no. 1939.6.15.65.

Dammer I., Banda Sea; 16–27 metres; Admiralty; the holotype of *T. ajax* Livingstone, no. 92.4.4.24.

SYNONYMY. Unfortunately Livingstone had only photographs upon which to base his two nominal species, *Tamaria propetumescens* and *ajax*, and was unable to handle personally these and the other relevant specimens in the British Museum collections. The five individuals from Parry Shoal, including the holotype of *T. propetumescens*, show a range of variation in the armament of the central parts of the convex abactinal plates from almost as fine as the peripheral granules (as in the type of *T. propetumescens*) through somewhat coarser granulation (as in the type of *tumescens*) to markedly coarser with often a single enlarged flattened or conical tubercle (as in the type of *ajax* from the Banda Sea). H. L. Clark (1938) has already referred *T. propetumescens* to the synonymy of *T. tumescens* and I consider that the holotype of *T. ajax* also comes within the range of variation of the species.

Livingstone distinguished *T. propetumescens* from the holotype of *tumescens* by the more obvious demarcation of the marginal plates, the greater extent proximally of the subambulacral spines, their separation from the furrow spines by granulation and by the development of stout infero-marginal tubercles in the type of *propetumescens*. H. L. Clark found the infero-marginal armament to be very variable, while the marked separation of the marginal plates is due to shrinkage in the drying of Livingstone's type. Also I suspect that Koehler's artist omitted to draw the granules between the furrow and subambulacral spines since these are present in the other specimens in the British Museum collections but may be inconspicuous owing to contraction of the adambulacral plates. The extent and regularity of the subambulacral spines proximally are variable in other species of *Tamaria*.

As for *Tamaria ajax*, Livingstone believed this to be related to *T. triseriata* (Fisher) from the Hawaiian Islands and did not compare it with *T. tumescens*. However, it shares the distinctive broadened carinal row of plates so characteristic of *tumescens* with which the armament is much more closely comparable than is that of *triseriata*. The holotype of *ajax* is in spirit, which accounts for its smoother appearance in photographs than the type of *propetumescens*. The apparent difference in the pedicellariae of the two shown by C. C. A. Monro's drawings in Livingstone's paper is not constant, the valves being equally short and with inconspicuous teeth all round the expanded end in some pedicellariae of the type of *propetumescens* as in the one shown for *ajax*.

Ophidiaster helicostichus Sladen

Linckia nodosa : Bell, 1884 : 124 [Non *L. nodosa* Perrier, 1875, which is a synonym of *L. bouvieri*.]
Ophidiaster helicostichus Sladen, 1889 : 405–407, pl. lxix, figs. 5–7.
Hacelia helicostichus : H. L. Clark, 1909 : 111 ; 1921 : 86 ; 1938 : 139 ; 1946 ; 122–123.
Tamaria sp. Livingstone, 1932 : 261–262 (at least the specimen in pl. xi, figs. 5, 6).
?*Ophidiaster astridae* Engel, 1938 : 12–14, figs. 2–4, pl. iii, fig. 3.

MATERIAL. " Challenger " station 187, Booby I., Torres Strait ; 11 metres ; the holotype, B.M. reg. no. 90.5.7.618.

Cape York, N. Queensland ; Mr. Damel ; 1 specimen, no. 67.5.27.1.

Prince of Wales Channel, Torres Strait ; 13 metres ; Admiralty (H.M.S. " Alert "); 2 specimens, no. 82.2.22.22 and 23.

N.W. Australia ; Admiralty ; 1 specimen, no. 92.1.14.76.

Holothuria Bank, northern Australia ; Admiralty (H.M.S. " Penguin ") ; 1 specimen, no. 92.1.14.69. Holothuria Bank ; 40 metres ; 1 specimen, no. 92.1.14.238.

Port Molle, Queensland ; 26 metres ; Admiralty (H.M.S. " Alert ") ; 1 specimen, no. 81.10.26.125–127. Port Molle ; presented by Sydney Museum ; 1 specimen, no. 83.12.9.88.

AFFINITIES. In 1909, following receipt of a British Museum specimen from Prince of Wales Channel (" Alert "), H. L. Clark commented " There can be no question, I think, that this species is congeneric with *Hacelia attenuata* Gray from the Mediterranean". In his key to the genera of Ophidiasteridae (1921) he distinguished *Hacelia* as having ten series of pore-areas on each arm, the lowest one each side situated between the adjacent rows of actinal plates and so more numerous than the others. This is true enough of *H. attenuata* and evidently also of Koehler's variety *inarmatus* of *helicostichus* (1885) from the Sunda Islands, which was raised to specific rank by H. L. Clark (1921). However, in 1938 Dr. Clark referred another Australian specimen to *helicostichus* and noted that " the actinal papulae are poorly developed and only here and there at isolated spots can one count ten (or even nine!) longitudinal series of papulae". There are nine specimens of *helicostichus* in the British Museum collections, six of them with R > 100 mm., including two from the same station as the one sent to H. L. Clark in 1909. In none of these can I find more than eight series of papular areas, the lowest of which are between the infero-marginal plates and the outermost series of actinals. Similarly in 1946, D. D. John of this museum could find no interactinal papulae in the six larger specimens when he examined them at the request of Dr. Engel. Nothing appears to have been published by Engel concerning this but in 1938 he had described a large sea-star (R up to 220 mm.) from the East Indies as *Ophidiaster astridae*. This is clearly closely related to, if not conspecific with, *helicostichus* ; his description and figures bring out no way in which the two can be distinguished.

In view of this, I consider that there are insufficient grounds for treating *helicostichus* as congeneric with *Hacelia attenuata* and accordingly refer it back to *Ophidiaster*. It differs from the Mediterranean and Atlantic type-species, *O. ophidianus*, in having more numerous series of actinal plates, about four proximally when R = 100–150 mm., rather than two, and the area covered by these plates is correspondingly more extensive. However, several of the Indo-Pacific species of *Ophidiaster*, such as *O. hemprichi*, approximate to *helicostichus* in the number and extent of the actinal plates, though they do not reach nearly such a large size.

Immature specimens of *O. helicostichus* (R < c. 70 mm.) with the lowest series of pore-areas below the infero-marginals barely developed or even lacking, may be confused with *Tamaria* but can be distinguished from the Australian species of that genus by the more attenuated arms. The specimen with R 103·5 mm. from Port Curtis, Queensland, shown in Livingstone's pl. xi, figs. 5 and 6 (1932) under the caption of " *Tamaria* sp. " is almost certainly conspecific with *helicostichus*, resembling closely the two specimens from Port Molle, Queensland (R 50–57 mm.) and a smaller one (R 36 mm.) from Holothuria Bank, which I have referred to this species. The incipient pore-areas below the infero-marginals (which prompted Livingstone's doubts about the validity of *Tamaria* as a genus distinct from *Ophidiaster*), the faint grooving of the furrow spines and their alternation in size (though this is admittedly a general tendency in *Tamaria*) as well as the form of the skeleton with its even armament of granules, are all as would be expected in *helicostichus* at this size.

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PLATE 1

FIGS. 1–3. *Gomophia egyptiaca egeriae* subsp. nov., holotype, B.M. reg. no. 92.8.22.52, aboral (1) and oral (2) views, with detail of denuded arm (3).

FIGS. 4, 5. The same, paratypes, no. 92.8.22.53 and 259, aboral views ; all from Macclesfield Bank.

FIG. 6. *Gomophia egyptiaca egyptiaca* Gray, no. 98.10.17.12, Christmas I., Indian Ocean, aboral view.

FIGS. 7, 8. The same, no. 67.1.7.42, Samoa, side view of denuded arm (7) and aboral view (8), in (7) the lowest series of plates is the infero-marginal one.

FIG. 9. *Nardoa frianti* Koehler, no. 92.8.22.264, Macclesfield Bank, aboral view.

FIG. 10. The same, no. 98.8.8.53, Loyalty Is., aboral view.

All approximately × $\frac{2}{3}$ except (2) × $2\frac{1}{3}$ and (7) × $1\frac{1}{3}$.

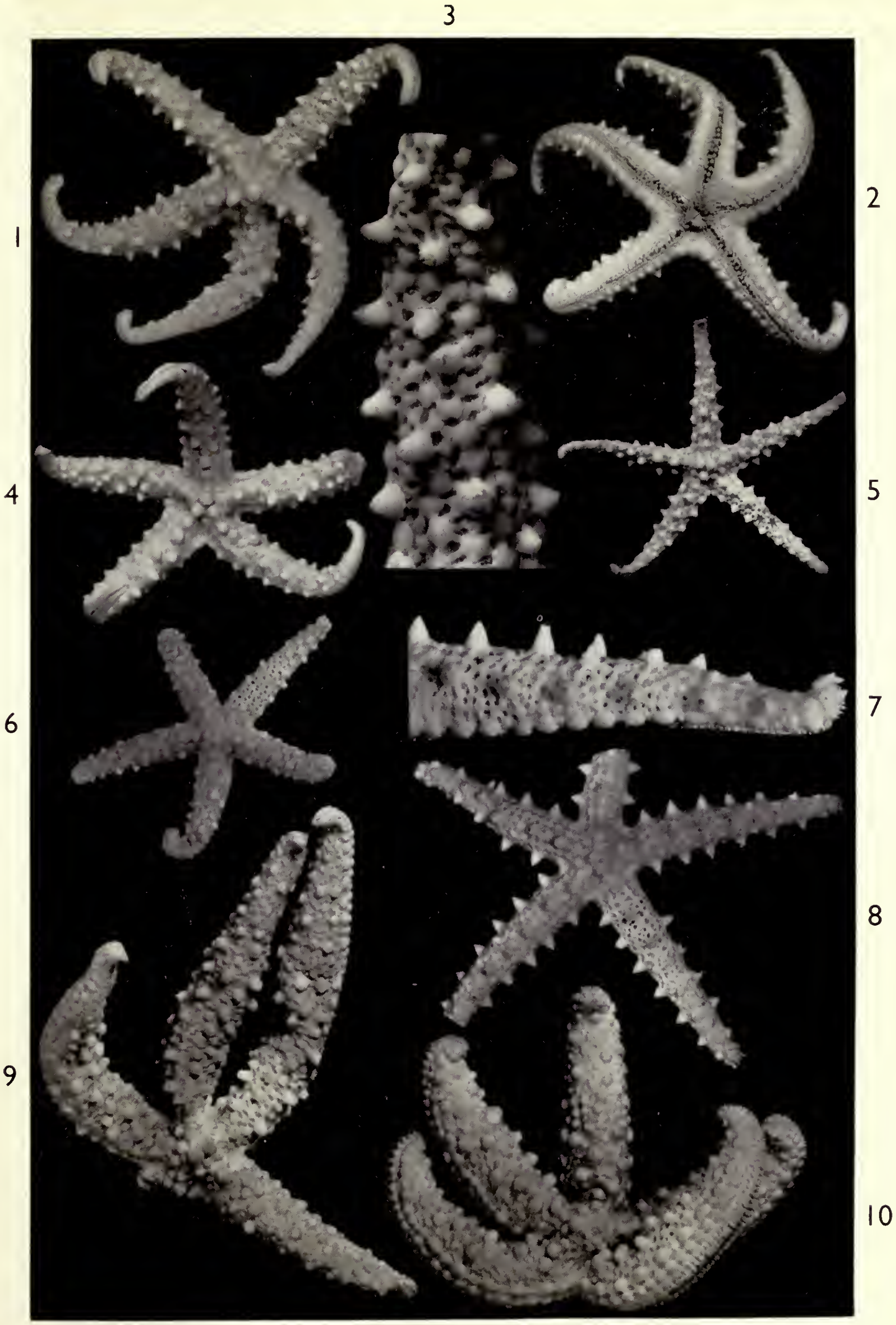
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PLATE 2

FIGS. 1–4. *Nardoa gomophia* (Perrier), holotype, B.M. reg. no. 59.4.25.3, New Caledonia, aboral (1) and oral (2) views, both × $\frac{2}{3}$, detail of denuded arm (3), × 2$\frac{1}{3}$ and side view of arm (4), × 1$\frac{1}{3}$.

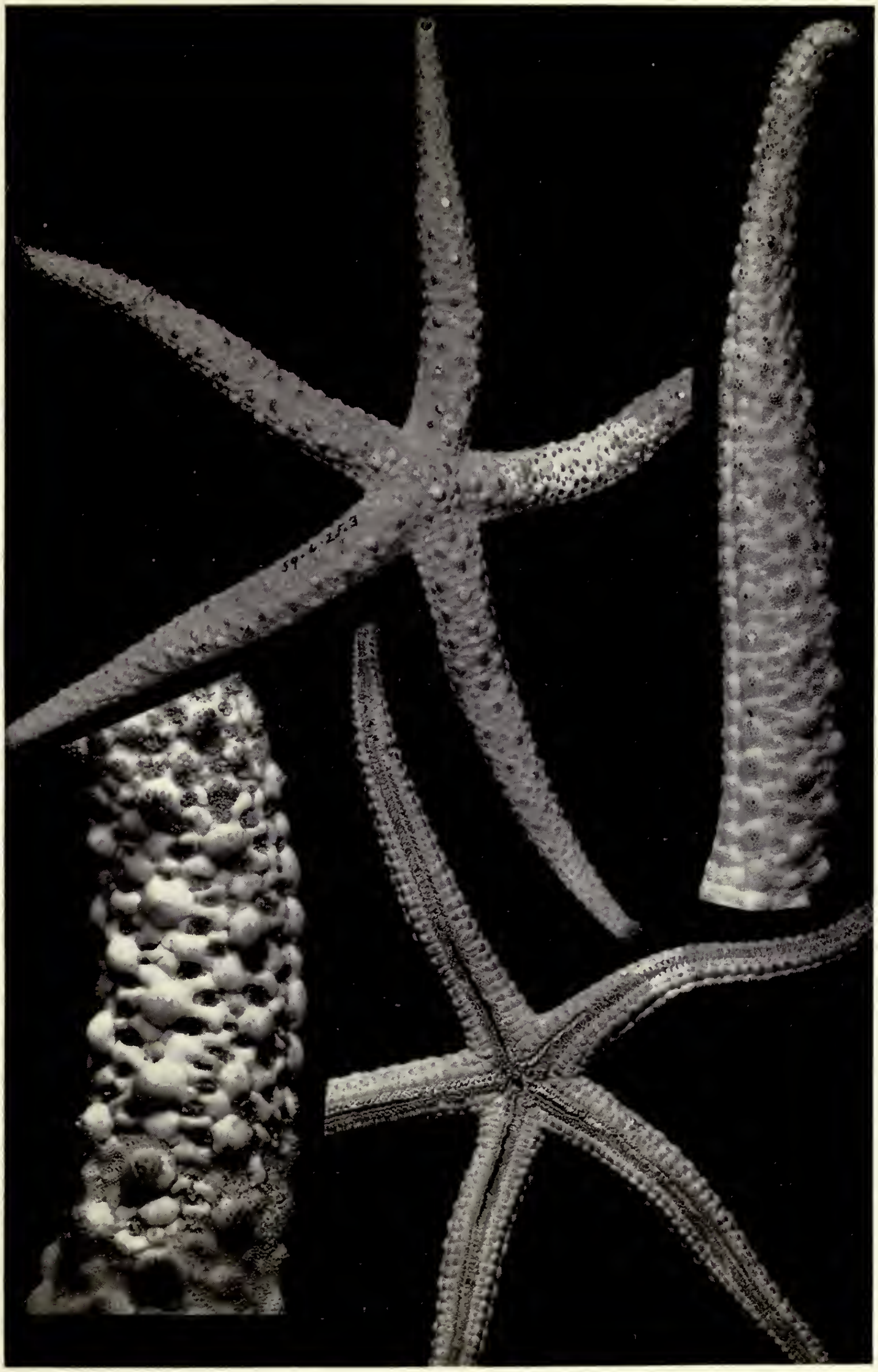
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PLATE 3

Figs. 1–3. *Nardoa sphenisci* sp. nov., holotype, B.M. reg. no. 92.1.14.27, Holothuria Bank, N.W. Australia, aboral (1) and oral (2) views, both × $\frac{2}{3}$ and side view of partly denuded arm (3), × 2.

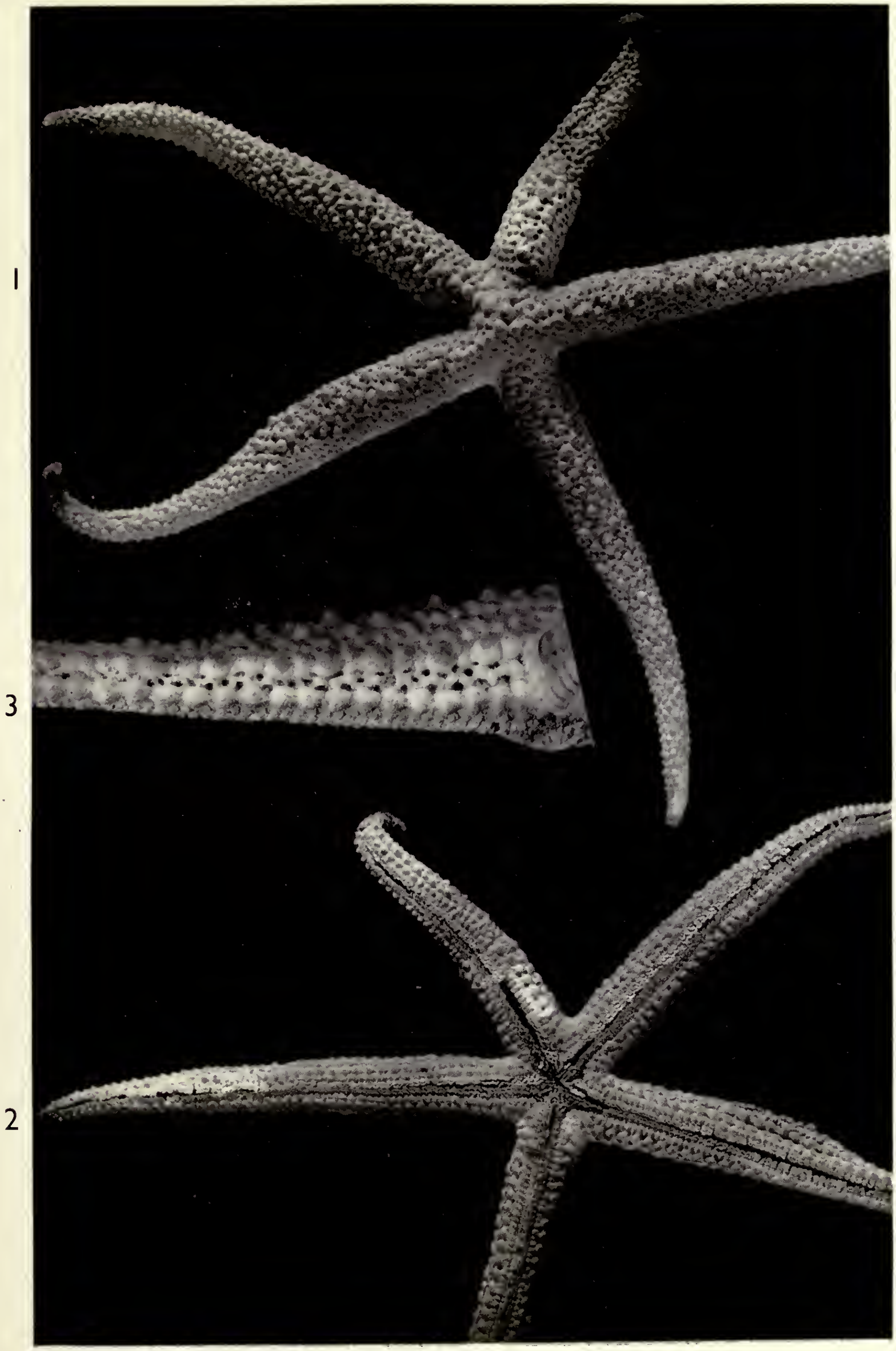
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PLATE 4

FIG. 1. *Nardoa tuberculata* Gray, holotype, B.M. reg. no. 1938.6.23.4, Sual, Philippine Is., aboral view, × $\frac{2}{3}$.

FIGS. 2, 3. The same, holotype of *Scytaster obtusus* Perrier, no. 43.3.29.6, Siguijor, Philippine Is., aboral view (2), × $\frac{2}{3}$ and side view of arm (3), × $1\frac{1}{3}$.

FIG. 4. *Nardoa* sp. aff. *tuberculata*, no. 1949.2.14.16, Batjan, Molucca Is., aboral view, × $\frac{2}{3}$.

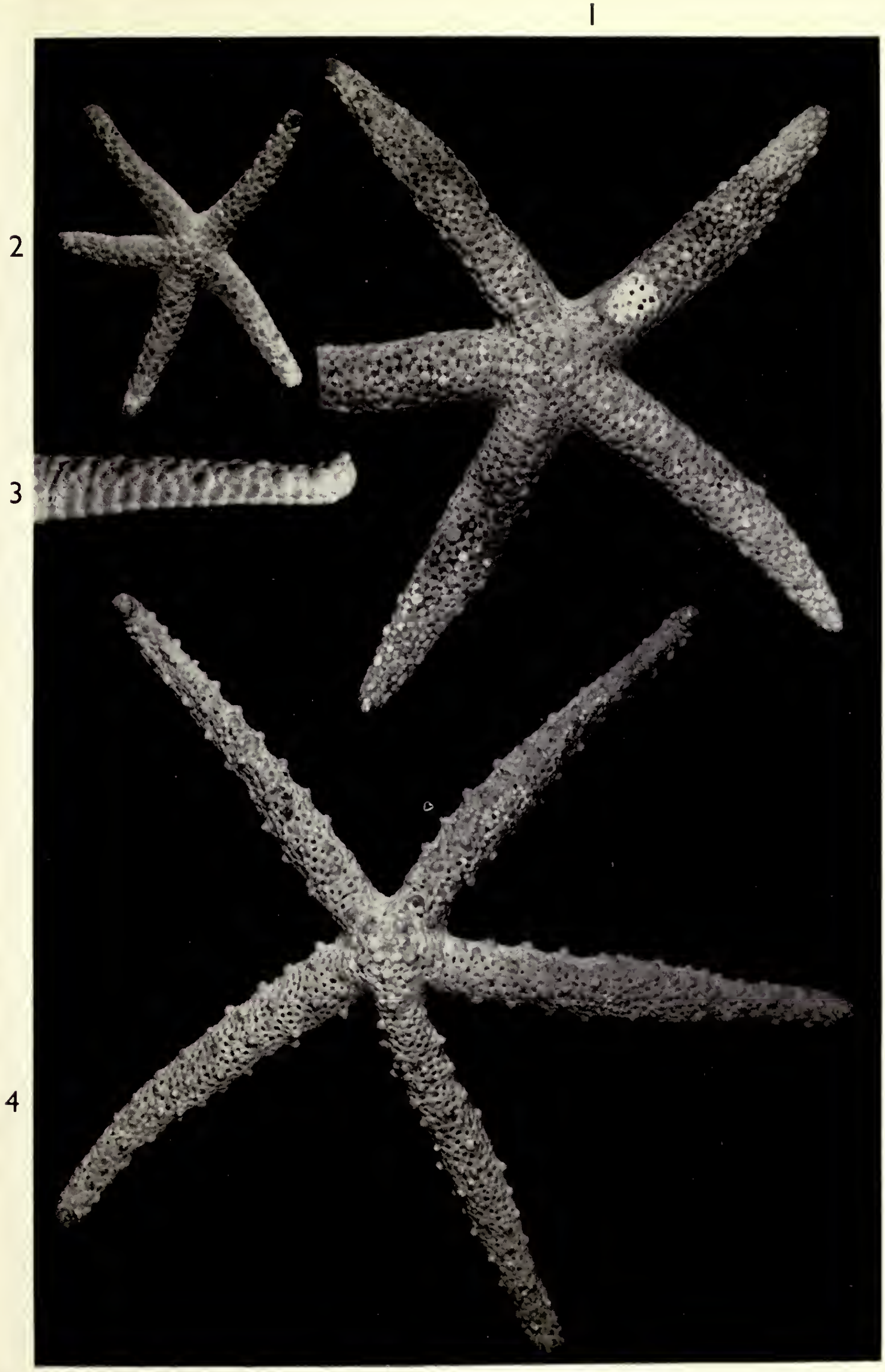
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PLATE 5

FIG. 1. *Nardoa novaecaledoniae* (Perrier), Oslo Museum collection, New Caledonia, aboral view, × $\frac{2}{3}$.

FIG. 2. The same, B.M. reg. no. 59.4.25.4, New Caledonia, previously labelled as holotype of *N. gomophia*, aboral view, × $\frac{2}{3}$.

FIG. 3. *Nardoa rosea* H. L. Clark, paratype, no. 1966.7.14.1, Mer, Torres Strait, side view of the single arm, × $1\frac{1}{3}$.

FIG. 4. The same, paratype, Museum of Comparative Zoology, Harvard collection, no. 2326, Mer, detail of partly denuded arm, × $1\frac{1}{3}$.

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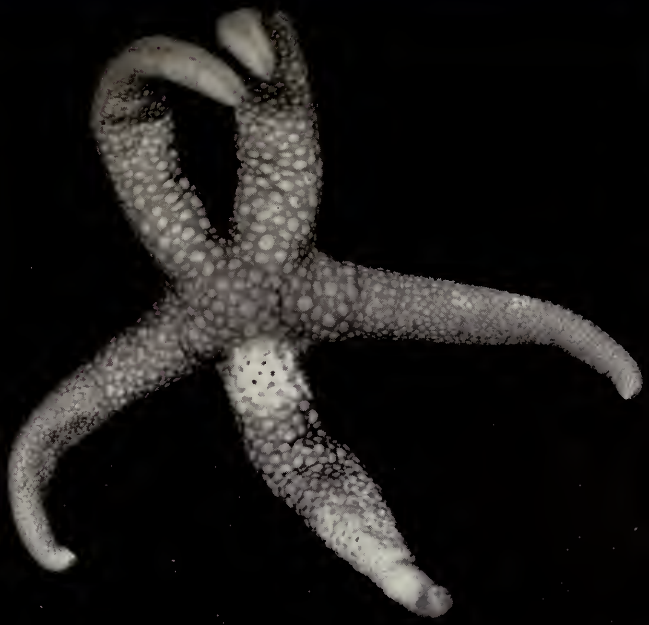

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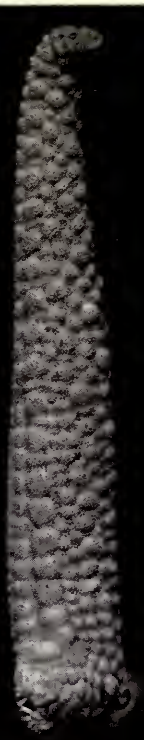

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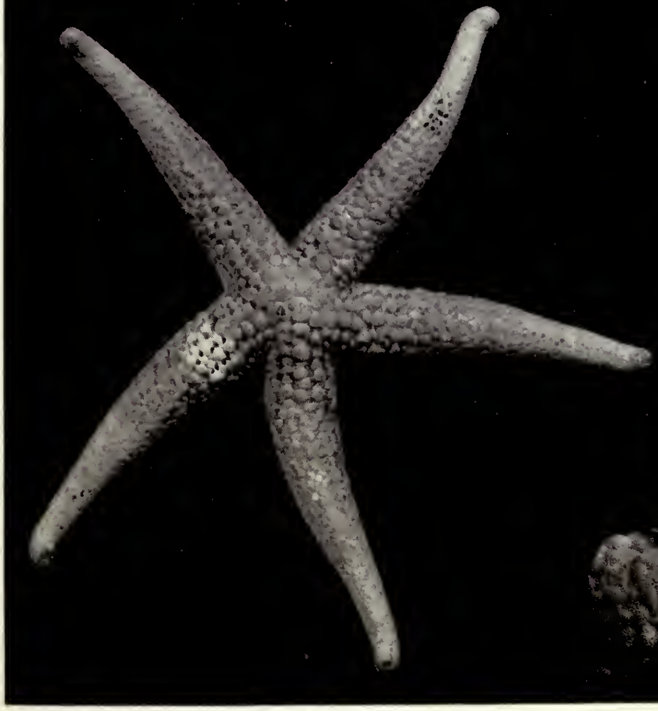

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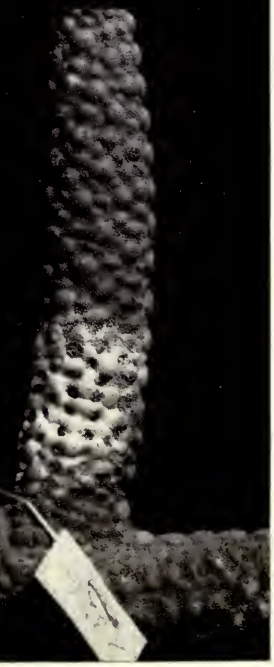


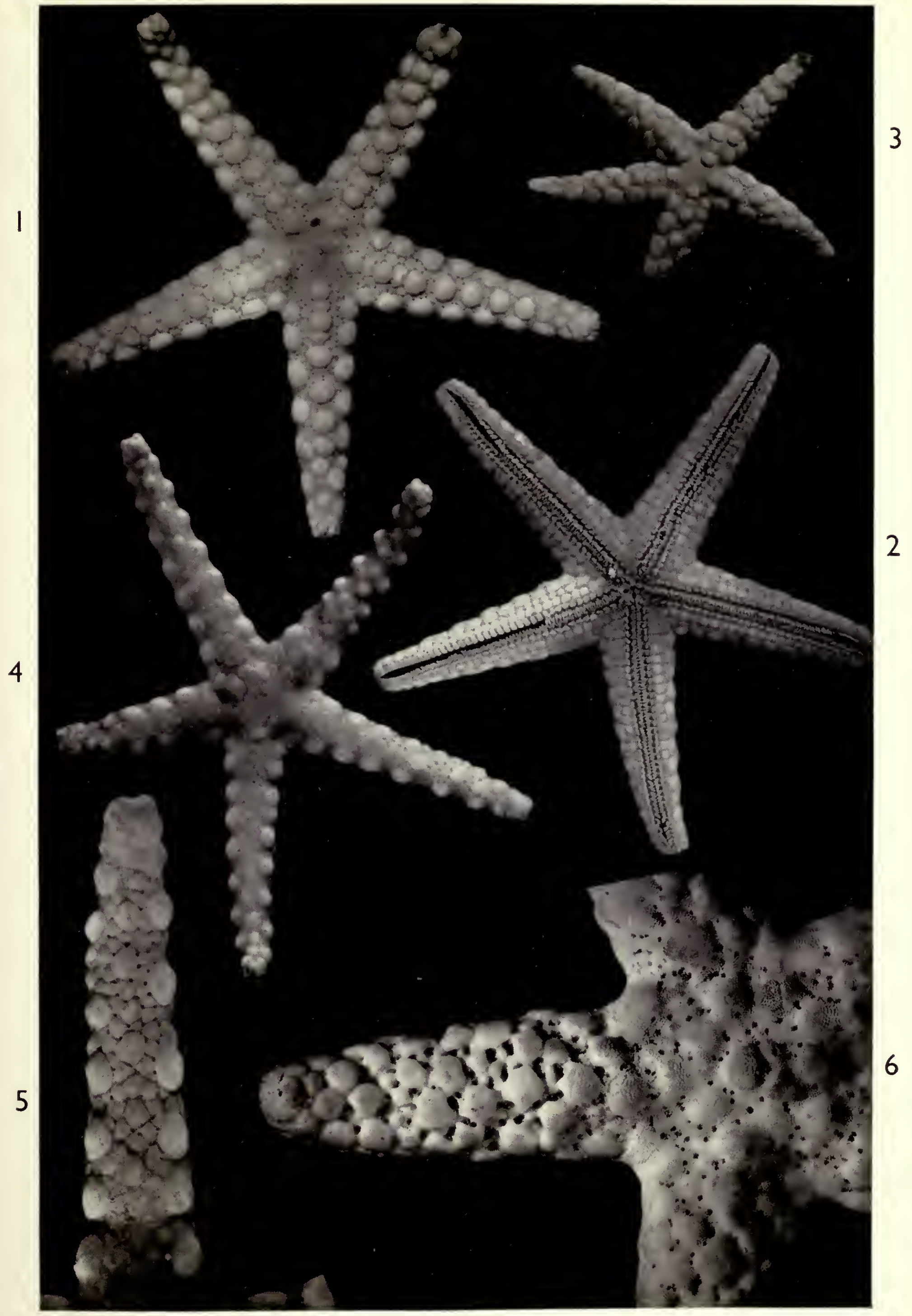
PLATE 6

FIGS. 1, 2. *Fromia nodosa* sp. nov., holotype, B.M. reg. no. 1907.7.1.95, Amirante Is., aboral (1) and oral (2) views, both × $1\frac{1}{3}$.

FIG. 3. The same, Cambridge Museum collection, S. Nilandu, Maldive Is., aboral view, × $\frac{2}{3}$.

FIGS. 4, 5. *Celerina heffernani* (Livingstone), no. 93.8.25.90, Macclesfield Bank, S. China Sea, aboral view (4), × $1\frac{1}{3}$ and detail of denuded arm (5), × $2\frac{2}{3}$.

FIG. 6. *Ferdina flavescens* Gray, holotype, no. 1938.6.23.7, Mauritius, detail of denuded arm and part of disc, × $2\frac{1}{2}$.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Pp. 199–225 ; 17 *Plates*

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NEW SPECIES OF *STELLICOLA* (COPEPODA, CYCLOPOIDA) ASSOCIATED WITH STARFISHES IN MADAGASCAR, WITH A REDESCRIPTION OF *S. CAERULEUS* (STEBBING, 1900)

By ARTHUR G. HUMES & JU-SHEY HO

INTRODUCTION

Two species of the lichomolgid genus *Stellicola* (a genus usually living in association with asteroid echinoderms) are known from starfishes in the region of Nosy Bé, in northwestern Madagascar. *S. oreastriphilus* Kossmann, 1877, occurs commonly on *Protoreaster lincki* (Blainville), *Culcita schmideliana* (Retzius), *Pentaceraster mammillatus* (Audouin), and *Poraster superbus* (Möbius) (Humes & Cressey, 1961), and more rarely on *Choriaster granulatus* (Lütken) (Humes & Ho, in press). A second species of *Stellicola*, whose description by Humes and Ho is in press, also occurs on *Choriaster granulatus*. Five new species from the region of Nosy Bé are now to be added, bringing the total number of species in that area to seven.

The field work was done by the first author, in 1960 while a member of an expedition sent to Madagascar by the Academy of Natural Sciences of Philadelphia, and in 1963–64 while participating in the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the material has been aided by a grant (GB-1809) from the National Science Foundation of the U.S.

We wish to thank Dr. H. Barraclough Fell and Mr. James F. Clark of the Museum of Comparative Zoology, Harvard University, for the identifications of the starfishes collected in 1963–64 (with the exception of the *Retaster cribrosus* from Ankify which was determined by Dr. G. Cherbonnier of the Muséum National d'Histoire Naturelle in Paris) and Dr. Elisabeth Deichmann, also of the Museum of Comparative Zoology, for determining the starfishes collected in 1960. It is a pleasure also to acknowledge the assistance given to the field work by the staff at the Centre d'Océanographie et des Pêches et Nosy Bé during the eighteen months while the first author was resident there.

We are also indebted to Dr. J. P. Harding of the British Museum (Natural History) for information on the whereabouts of Thompson and A. Scott's Ceylonese copepods and to Miss Patricia D. Lofthouse of the same museum for arranging the loan of syntypes of *S. caeruleus* with permission to dissect a male and a female.

The material covered in this paper comprises :

Stellicola kossmanni, new species
Stellicola affinis, new species
Stellicola longiseta, new species
Stellicola femineus, new species
Stellicola pollex, new species
Stellicola oreastriphilus Kossmann, redescription in part
Stellicola caeruleus (Stebbing), redescription of syntypes

STELLICOLA Kossmann, 1877

Stellicola kossmanni n. sp.

Pl. 1, figs. 1–6; Pl. 2, figs. 7–15; Pl. 3, figs. 16–21; Pl. 4, figs. 22–24.

TYPE MATERIAL. 4 ♀ and 14 ♂ from washings of 83 starfishes, *Protoreaster lincki* (Blainville), in a depth of 0·5 m. at Pte. Antsamantsara, west of Madirokely, Nosy Bé, Madagascar. Collected 7th July, 1963. Holotype female, allotype, and 13 paratypes (2 ♀, 11 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.1–3; the remaining 3 paratypes (dissected) in the collection of A. G. Humes.

Other specimens (all from *Protoreaster lincki* in 0·5 m.). 6 ♀, 6 ♂ from 7 hosts, Pte. Mahatsinjo, Nosy Bé, 4th July, 1963; 1 ♀, 6 ♂ from 60 hosts at Pte. Lokobe, Nosy Bé, 11th July, 1963.

FEMALE. Body (Pl. 1, fig. 1) with moderately broadened prosome. Length (not including setae on caudal rami) 1·0 mm. (0·95–1·03 mm.) and greatest width 0·46 mm. (0·44–0·47 mm.), based on 10 specimens (holotype, 3 paratypes, and 6 specimens from Pte. Mahatsinjo, 4th July, 1963). Ratio of length to width of prosome 1·45 : 1. Segment of leg 1 separated dorsally and laterally from head by a furrow. Epimeral areas of segments of legs 1–4 rounded; lateral margins of segments of legs 1–3 with membrane (Pl. 1, fig. 2).

Segment of leg 5 (Pl. 1, fig. 3) 83 μ long and 105 μ in greatest width; fifth legs borne slightly dorsally. Between this segment and genital segment a short intersegmental sclerite ventrally. Genital segment longer than wide, 146 μ in length, 127 μ in width in its anterior three-fourths where its lateral margins are somewhat irregular, and 85 μ in width in its constricted posterior fourth. Areas of attachment of egg sacs situated dorsolaterally just in front of posteriormost fourth; each area (Pl. 1, fig. 4) with 2 long setae (outer 82 μ long and bearing minute unilateral spinules, inner 36 μ and feathered) and between them a small spinous process 6 μ long. Posterior margin of segment with a membrane having a ragged edge simulating small spinules especially laterally. Three postgenital segments, first 44 × 75 μ with a similar posterior membrane, second 18 × 68 μ, and third 28 × 65 μ.

Caudal ramus (Pl. 1, fig. 5), inserted ventrally on anal segment, quadrate, 31 × 29 μ. Long naked setule (34 μ) midway on outer margin. Pedicellate dorsal seta 65 μ and haired. Outer lateral seta 109 μ and naked, inserted close to outermost terminal seta (156 μ, with a few spinules on each side in its proximal third). Innermost terminal seta 216 μ and naked. Two long terminal setae, inserted between dorsal (smooth) and ventral (with a row of prominent setules) flaps, 429 μ (outer) and 600 μ (inner) and both with lateral spinules; "pegged" region of these two setae finely punctate. A small hair on ventral surface of ramus.

Dorsal surface of prosome with scattered hairs (sensilla). Dorsal surface of urosome with hairs as shown in Pl. 1, fig. 3; ventral surface less ornamented with hairs. Ratio of length of prosome to that of urosome 1·87 : 1.

Egg sac (Pl. 1, fig. 1) elongated, 520 × 275 μ, extending far beyond caudal rami, and containing many eggs about 50 μ in diameter.

Rostral area (Pl. 1, fig. 6) rounded, not strongly sclerotized.

First antenna (Pl. 2, fig. 7) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 39 (50 μ along anterior margin), 74, 31, 41, 34, 18, and 16 μ respectively. Formula for armature: 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae naked except 1 on second segment and 4 on last 3 segments which are delicately haired. Terminal seta on segment 7 very long (260 μ), equal to length of entire first antenna. Aesthete on segment 7 arising from common base with adjacent long naked seta. Ventral surface of segment 3 with sclerotization suggesting an intercalary segment.

Second antenna (Pl. 2, fig. 8) relatively slender and 3-segmented, third segment showing a partial division on anterior surface but entire posteriorly. First segment with a smooth seta, second with a haired seta, and third with 3 haired setae near the incomplete division and terminally with 6 elements: a stout claw 42 μ along its axis, 4 long naked setae, and a short blunt naked seta. Anterior surface of second antenna pilose, with 4 slender setules subterminally on last segment. Long setae annulated.

Labrum (Pl. 2, fig. 9) with its two posteroventral lobes somewhat angular and unornamented.

Mandible (Pl. 2, fig. 10) with an outer row of slender spinules and an inner row of rather stout blunt teeth preceded proximally by a prominent dentiform process; both rows diminishing to minute spinules along the slender terminal lash. Paragnath a small lobe hidden under lobe of labrum in ventral view. First maxilla (Pl. 2, fig. 11) an elongated lobe with 3 naked setae and 1 stout spiniform element strongly spinose on its posterolateral surface. Second maxilla (Pl. 2, fig. 12) 2-segmented; first segment unarmed, its proximal ventral margin projecting strongly; second segment with 2 postero-inner elements (a slender seta with short lateral spinules and a spine with rows of spinules) and terminating in a spiniform process bearing rows of teeth as in the figure (proximal tooth larger than others, producing a bifurcated appearance). Maxilliped (Pl. 2, fig. 13) 3-segmented; first segment unarmed, second with 2 setae and anterior surficial spinules, and third with 2 setae (1 with lateral spinules, other naked) and terminating in a spiniform process bearing lateral spinules.

Area between maxillipeds and first pair of legs (Pl. 2, fig. 14) not protuberant, with a distinct sclerotized line between bases of maxillipeds.

Rami of legs 1–4 (Pl. 2, fig. 15, Pl. 3, figs. 16, 17, and 18) 3-segmented, except endopod of leg 4 which is weakly 2-segmented. Spine and setal formula as follows (Roman numerals indicating spines, Arabic numerals setae):

P_1	protopod	0–1;	1–0	exp	I–0;	I–1;	III, I, 4
				end	0–1;	0–1;	I, 5
P_2	protopod	0–1;	1–0	exp	I–0;	I–1;	III, I, 5
				end	0–1;	0–2;	I, II, 3
P_3	protopod	0–1;	1–0	exp	I–0;	I–1;	III, I, 5
				end	0–1;	0–2;	I, II, 2
P_4	protopod	0–1;	1–0	exp	I–0;	I–1;	II, I, 5
				end	0–1;	II, 1	

Inner seta on coxa feathered in legs 1–3 but naked (42 μ long) in leg 4. Hairs on inner margin of basis in legs 1–3 absent in leg 4. Expansion of basis over anterior surface of first segment of exopod rather acute. Between 2 terminal spines on last segment of endopod of leg 2 a bifurcated spinous process. On second segment of exopod of leg 4 relatively short inner seta lying (in alcoholized specimens) nearly parallel to ramus and having short lateral spinules instead of the usual long hairs. Endopod of leg 4 two-segmented, with a line of separation visible on both anterior and posterior surfaces, but with the lateral sclerotization continuous between the two segments. First segment 26 × 24 μ (greatest dimensions) with inner distal seta 84 μ long, spiniform, with short lateral spinules. Second segment 46 × 21 μ (greatest dimensions), the feathered inner seta 67 μ, the 2 terminal spines 105 μ (inner) and 58 μ (outer) both with delicately serrate lamellae; a row of minute spinules anteriorly across end of segment near insertions of 2 spines, and a row of hairs on proximal half of outer margin of segment.

Leg 5 (Pl. 3, fig. 19) with free segment elongated, 32 × 14 μ. Two very unequal terminal setae, outer 102 μ long, with minute lateral spinules, inner 55 μ, with delicately serrate lamellae. Seta on body near insertion of free segment 40 μ and feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 1, figs. 3 and 4).

Colour in life in transmitted light faintly reddish, eye red, intestine dark brown, ovary reddish brown.

MALE. Body form (Pl. 3, fig. 20) resembling that of female, though prosome somewhat narrower. Length (excluding setae on caudal rami) 0·71 mm. (0·69–0·74 mm.) and greatest width 0·27 mm. (0·26–0·28 mm.), based on 10 specimens. Ratio of length to width of prosome 1·72 : 1.

Segment of leg 5 (Pl. 3, fig. 21) 33 × 70 μ. Ventral intersegmental sclerite absent. Genital segment about as long as wide, 99 × 94 μ, with slightly rounded lateral margins in dorsal view. Four postgenital segments 42 × 66, 34 × 58, 11 × 50, and 21 × 52 μ from anterior to posterior.

Caudal ramus like that of female but smaller, 23 × 23 μ.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 1·85 : 1.

Rostral area, first antenna, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla like those of female. Maxilliped (Pl. 4, fig. 22) slender and 4-segmented. First segment unarmed, second with 2 naked setae and 2 rows of spinules, and third small and unarmed. Proximal part of terminal claw probably representing fourth segment. Claw 101 μ in length (measured along its axis), recurved, showing a slight evidence of division about midway and having a fringe of delicate hyaline spinules along its concave edge; bearing 2 setae proximally, one small naked and hyaline 12 μ long, other long (50 μ) with a few distal spinules.

Area between maxillipeds and first pair of legs like that in female.

Legs 1–4 resembling those of female, with same spine and setal formula. Endopod of leg 4 with 2 terminal spines differing in their proportional lengths. Measurements for this ramus : first segment 19 × 18 μ with seta 66 μ, second segment 33 × 17 μ with seta 45 μ and 2 terminal spines 80 μ and 47 μ (ratio of these 2 spines 1·7 : 1, instead of 1·8 : 1 in female).

Leg 5 resembling that of female, with free segment 21 × 8 μ and 2 terminal elements 70 μ and 34 μ respectively.

Leg 6 (Pl. 4, fig. 23) consisting of posterolateral flap on ventral surface of genital segment and bearing a minute spiniform process and 2 unequal setae, one naked (69 μ), other feathered (33 μ). In view of entire urosome these setae conspicuous (see Pl. 3, fig. 21).

Spermatophore (Pl. 4, fig. 24), inside body of male, elongated, 86 × 31 μ without neck.

Colour in life in transmitted light resembling that of female.

(This species is named for Dr. Robby Kossmann, who originally described the genus *Stellicola*).

Comparison with related species. There are at present fifteen species known with some certainty to belong to the genus *Stellicola* (14 with published descriptions and 1 whose description by Humes and Ho is in press). Stock (1957) included *S. thorelli* Kossmann, 1877, *S. pleurobranchi* Kossmann, 1877, *S. oreastriphilus* Kossmann, 1877, *S. caeruleus* (Stebbing, 1900), *S. curticaudatus* (Thompson & A. Scott, 1903), *S. gracilis* (Thompson & A. Scott, 1903), *S. lankensis* (Thompson & A. Scott, 1903), and *S. asterinae* (Bocquet, 1952), a species later synonymized with *S. clausi* (Rosoll, 1889) by Bocquet and Stock (1962). The four West African species (*S. frequens*, *S. astropectinis*, *S. luidiae*, and *S. lautus*) originally described by Humes & Cressey (1958) in the genus *Lichomolgus* also belong to *Stellicola*, as pointed out by Bocquet and Stock (1962). In *Stellicola* there should also be included *S. holothuriae* (Ummerkutty, 1961) and probably *S. longicaudatus* (Thompson & A. Scott, 1903).

S. kossmanni may be separated from these fifteen species as follows : in *gracilis*, *lankensis*, and the new species of Humes & Ho (in press) there are two postgenital segments in the female and three in the male ; in *frequens*, *astropectinis*, *luidiae*, and *lautus* there are three claws on the second antenna ; in *clausi* there are two claws on the second antenna ; and in *oreastriphilus*, *holothuriae*, *thorelli*, *pleurobranchi*, *curticaudatus*, *longicaudatus*, and *caeruleus*, although the second antenna has only a single claw, the length ratio of prosome to urosome in the female (ranging from 2·3–3·3 : 1) is distinctly more than 2 : 1.

S. kossmanni shows several features which may be used as identifying characters : the very long terminal seta on the first antenna (as long as the antenna itself), the four slender subterminal setules on the second antenna (these in addition to the six terminal elements), the strongly spinose element on the first maxilla, and in leg 4 the detailed ornamentation of the four elements on the endopod and the nature of the inner seta on the second segment of the exopod.

Stellicola affinis n. sp.

Pl. 4, figs. 25–31; Pl. 5, figs. 32–41; Pl. 6, figs, 42–48.

TYPE MATERIAL. 84 ♀ and 26 ♂ washed from 2 starfishes, *Maculaster maculata maculata* (Müller & Troschel), exposed on sand bar at low tide on the eastern side of Ankify, on the mainland of Madagascar, opposite Nosy Komba, and about 15 kilometers south of Nosy Bé. Collected 8th August, 1964. Holotype female, allotype, and 51 paratypes (40 ♀, 11 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.4–6; 27 paratypes (20 ♀, 7 ♂) in the United States National Museum, Washington; and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all in the vicinity of Nosy Bé). From *Maculaster maculata maculata*: 16 ♀, 8 ♂ from 1 host, exposed on sand bar at Ankify (the type locality), 9th September, 1964. From *Maculaster savignyi* (Audouin): 38 ♀, 6 ♂ from 9 hosts, exposed on sand bar at Ankify, 8th August, 1964; 60 ♀, 27 ♂ from 1 host, in 2 m., eastern shore of Ambariobe, a small island between Nosy Komba and Nosy Bé, 4th October, 1964; 12 ♀, 3 ♂ from 1 host, on sand exposed at low tide, Ambariobe, 21st July, 1963. From *Retaster cribrosus* von Martens: 11 ♀, 5 ♂ from 1 host, exposed on sand bar, Ankify, 2nd November, 1963. From *Luidia maculata* Müller & Troschel: 35 ♀, 16 ♂ from 2 hosts, dredged in 17 m., 13° 16′ S, 48° 31′ 30″ E, northeast of Nosy Faly, 14th September, 1960.

FEMALE. Body (Pl. 4, figs. 25 and 26) relatively slender. Length (not including setae on caudal rami) 1·01 mm. (0·98–1·04 mm.) and greatest width 0·35 mm. (0·32–0·37 mm.), based on 10 specimens. Ratio of length to width of prosome 1·56 : 1. Epimeral areas of segment of leg 4 pointed.

Segment of leg 5 (Pl. 4, fig. 27) 61 × 97 μ. Between this segment and genital segment a short intersegmental sclerite ventrally. Genital segment elongated, 156 μ in length, being somewhat wider in its anterior two-thirds (109 μ) than in its posterior third (80 μ). Areas of attachment of egg sacs located dorsolaterally on anterior part of middle third; each area (Pl. 4, fig. 28) bearing 2 short naked setae (outer 13 μ long, inner 17 μ), with a small spinous process about 5 μ long between them. Two postgenital segments, first 56 × 63 μ, second (anal) 43 μ long and 72 μ in greatest width (this segment deeply incised).

Caudal ramus (Pl. 4, fig. 29) divergent, inserted a little ventrally on anal segment, elongated and somewhat narrowed distally, in one female 106 μ (greatest length) × 15 μ (width taken at level of outer seta) making a ratio of 7 : 1, in another female 108 × 17 μ, ratio of 6·3 : 1. Minute setule (4 μ long) on outer proximal margin. Another small setule (8 μ) on outer margin just beyond midpoint of ramus (perhaps corresponding to long marginal setule in *S. kossmanni*). Pedicellate dorsal seta 25 μ. Outer lateral seta 74 μ, inserted near end of ramus. Innermost terminal seta 130 μ, outermost terminal seta 88 μ, and 2 long median terminal setae, inserted between dorsal (smooth) and ventral (with a row of minute spinules) flaps, 242 μ (outer) and 363 μ (inner). All setae naked. Both outer and inner walls of ramus with an interruption in sclerotization as shown in figure. Two minute hairs on ventral surface of ramus.

Dorsal surface of prosome with scattered hairs. Dorsal surface of urosome with hairs as shown in Pl. 4, fig. 27; ventral surface much less ornamented with hairs. Ratio of length of prosome to that of urosome 1·30 : 1.

Egg sac (Pl. 4, fig. 25) fairly elongated, 374 × 143 μ, extending not quite to the ends of caudal rami, and containing a moderate number of eggs about 50 μ in diameter.

Rostral area (Pl. 4, fig. 30) rounded.

First antenna (Pl. 4, fig. 31) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 30 (47 μ along anterior margin), 67, 23, 25, 31, 19, and 14 μ respectively. Formula for armature as in *S. kossmanni.* Setae naked except for 1 on antepenultimate segment, 1 on penultimate segment, and 2 on last segment which are delicately haired. Long terminal seta 213 μ in length, nearly as long as entire first antenna. Aesthete on last segment having a common base with adjacent seta. Sclerotization on ventral surface of segment 3 suggesting an intercalary segment.

Second antenna (Pl. 5, fig. 32) 3-segmented, with no evidence of division of third segment. Armature 1; 1; 3 + 5 + 1 claw, as in *S. kossmanni,* though relative lengths and fine ornamentation of setae different (compare Pl. 2, fig. 8 and Pl. 5, fig. 32). Claw 41 μ along its axis. Anterior surface of second antenna not pilose as in *S. kossmanni;* posterior surface with very fine punctations.

Labrum (Pl. 5, fig. 33) with subtriangular unornamented lobes.

Mandible (Pl. 5, fig. 34) in general resembling that of *S. kossmanni,* but first element in inner row of teeth less prominent and terminal lash relatively shorter. Paragnath a small indistinct lobe medial to insertions of mandible and first maxilla (Pl. 5, fig. 38). Four elements on first maxilla (Pl. 5, fig. 35), including spine with lateral rows of spinules. Second maxilla (Pl. 5, fig. 36) 2-segmented, with proximal ventral margin of unarmed first segment rather angularly produced; second segment with long inner spine having serrated flanges (with serrations especially prominent along distal flange) and with terminal process bifurcated as shown in figure. Maxilliped (Pl. 5, fig. 37) 3-segmented, with armature resembling that of *S. kossmanni;* second segment lacking rows of small spinules seen in that species.

Area between maxillipeds and first pair of legs only slightly protuberant (Pl. 4, fig. 26); a sclerotized line connecting bases of maxillipeds (Pl. 5, fig. 38).

Rami of legs 1–4 (Pl. 5, figs. 39, 40, 41, and Pl. 6, fig. 42) with same segmentation and spine and setal formula as in *S. kossmanni.* Inner seta on coxa relatively long and feathered in legs 1–3 but short (19 μ) and naked in leg 4. Hairs on inner margin of basis absent in leg 4 and apparently also in leg 1. In legs 1–3 expansion of basis over anterior surface of first segment of exopod with membranous tip; this expansion absent in leg 4. Second segment of exopod of leg 4 with inner seta like that in *S. kossmanni.* Endopod of leg 4 two-segmented, with distinct articulation between these segments. First segment 31 × 25 μ (greatest dimensions) with finely barbed inner seta 91 μ long. Second segment 50 × 24 μ (greatest dimensions), the inner seta finely barbed and 48 μ, the 2 terminal spines 62 μ (inner) and 51 μ (outer), both with delicately serrate lamellae. Rows of long hairs along outer margins of both segments, with row on second segment interrupted. Row of minute spinules on anterior surface across end of segment near insertions of 2 spines.

Leg 5 (Pl. 6, fig. 43) with elongated free segment, 28 × 13 μ. Two unequal terminal setae, outer 61 μ long with a few minute barbs distally, inner 39 μ with outer serrated fringe. Seta on body near insertion of free segment 25 μ long and delicately feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 4, fig. 28).

Colour in life in transmitted light slightly opaque, ovary dark gray, eye dark blackish red, egg sacs dark gray.

MALE. Body form (Pl. 6, fig. 44) resembling that of female but more slender. Length (without ramal setae) 0·78 mm. (0·75–0·82 mm.) and greatest width 0·22 mm. (0·21–0·23 mm.), based on 10 specimens. Ratio of length to width of prosome 1·84 : 1.

Segment of leg 5 (Pl. 6, fig. 45) 31 × 65 μ. Ventral intersegmental sclerite absent. Genital segment subquadrate, 133 × 117 μ, a little longer than wide, with lateral borders nearly parallel in dorsal view. Three postgenital segments 47 × 59, 43 × 46, and 26 × 46 μ from anterior to posterior.

Caudal ramus (see Pl. 6, fig. 45) resembling that of female, but proportionately more slender, 90 × 12 μ, with ratio of 7·5 : 1, and a little more narrowed in its distal half.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 1·16 : 1.

Rostral area, first antenna, second antenna, labrum, mandible, paragnath, and first maxilla like those of female. Second maxilla also resembling that of female but proximal ventral margin of first segment less produced and more rounded. Maxilliped (Pl. 6, fig. 46) slender and 4-segmented. First segment unarmed. Second segment with 2 slender naked setae and 2 rows of spinules (1 row short, consisting of only about 5 spinules.) Third segment short and unarmed. Proximal part of claw probably representing fourth segment. Slender gently recurved claw 111 μ along its axis, with evidence of division about midway and having a fringe of delicate hyaline spinules along its concave margin; bearing proximally 2 setae, one 11 μ and naked, other 29 μ long with a few minute barbs near its tip.

Area between maxillipeds and first pair of legs like that in female.

Legs 1–4 resembling those of female, with same spine and setal formula. Endopod of leg 4 much like that in female, with 4 elements from inner to outer 72, 35, 43, and 34 μ long.

Leg 5 (Pl. 6, fig. 47) with free segment 21 × 8 μ, more slender than in female, and 2 terminal setae more unequal, 53 μ and 22 μ (ratio of 2·4 : 1, instead of 1·56 : 1 in female).

Leg 6 (Pl. 6, fig. 48) consisting of posterolateral flap on ventral surface of genital segment and bearing 2 slender naked setae 25 and 38 μ long.

Spermatophores not observed.

Colour in life in transmitted light resembling that of female.

[The specific name *affinis*, Latin = adjoining or related, refers to the close similarity of this species with *Stellicola gracilis* (Thompson & A. Scott) as discussed below].

COMPARISON WITH OTHER SPECIES. At present there are three species known in the genus *Stellicola* which, like *S. affinis*, have two postgenital segments in the female and three in the male. These are *S. gracilis* (Thompson & A. Scott, 1903), *S. lankensis* (Thompson & A. Scott, 1903), and the species whose description by Humes and Ho is in press. *S. lankensis* (of which only the female is known), from washings of dredged invertebrates in Ceylon, has a much shorter caudal ramus (proportions of about 2·37 : 1 in T. & S.'s pl. XV, fig. 25). The new species of Humes and Ho differs in having a quadrate caudal ramus, in its smaller size (female 0·79 mm., male 0·64 mm.), and in many other features.

S. gracilis, from washings of dredged invertebrates in Ceylon, is known only from the original description and figures by Thompson & A. Scott. The existence of type material (the " several males and females " of Thompson & A. Scott) is extremely doubtful. The type specimens of *S. gracilis* were apparently deposited in the University of Liverpool, where Dr. W. A. Herdman, the author of the Report on Pearl Oyster Fisheries, was professor of natural history. An inquiry recently made by Dr. J. P. Harding of the British Museum to the Department of Oceanography of Liverpool University drew the reply that the Andrew Scott collection had been discarded. Our only available information on *S. gracilis* is, then, to be found in the brief original description.

When *S. affinis* is compared with *S. gracilis* certain similarities are obvious. The two species are of about the same length and have the same number of postgenital segments. In the female of both the anal segment is cleft deeply, the caudal rami are divergent, the genital segment has a similar shape, the second antenna appears to have the same general form, the base of the mandible is somewhat angular. and the first segment of the second maxilla seems to project. In the male of both the maxilliped is rather similar.

There exist, however, differences between the two species which in our opinion make it impossible to regard them as one and the same species. In the female of *S. gracilis* the proportions of the caudal ramus are about 4 : 1 (instead of 6·3 : 1 or 7 : 1 as in *S. affinis*), the two inner setae on the endopod of leg 4 are distinctly feathered (while in *S. affinis* these setae have very minute barbs), and (based on measurements of T. & S.'s pl. XV, fig. 1) the ratio of the length of prosome to urosome is 1 : 1 (1·30 : 1 in *S. affinis*) and the ratio of length to width of the prosome is 1·75 : 1 (1·56 : 1 in *S. affinis*). T. & S.'s pl. XV, fig. 4, shows only three elements on the first maxilla, but a fourth minute seta may have escaped their notice. They describe the tip of the second maxilla as " triangular, sharp and wedge-shaped ", illustrated on pl. XV, fig. 5, but their description is wanting in detail.

We conclude that *S. affinis*, while related to *S. gracilis*, is a separate species.

Stellicola longiseta n. sp.

Pl. 6, figs. 49–50; Pl. 7, figs. 51–60; Pl. 8, figs. 61–66.

TYPE MATERIAL. 2 ♀ and 3 ♂ from washings of 1 starfish, *Mithrodia clavigera* (Lamarck), under dead coral (*Acropora*) in a depth of 1 m., Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar. Collected 3rd September, 1963. Holotype female, allotype, and 2 paratypes (1 ♀, 1 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.7–9; the remaining paratypic male (dissected) in the collection of A. G. Humes.

Other specimens (from *Mithrodia clavigera* in the same locality). 2 ♀ from 1 host in 1 m., 14th December, 1963.

FEMALE. Body (Pl. 6, fig. 49) with prosome relatively thickened as in *S. affinis*, but broader than in that species. Length (excluding setae on caudal rami) 1·18 mm. (1·14–1·22 mm.) and greatest width 0·60 mm. (0·58–0·62 mm.), based on 4 specimens (holotype, 1 paratype, and 2 specimens collected on 14th December, 1963). Ratio of length to width of prosome 1·36 : 1. Segment of leg 1 separated from head by a dorsal and lateral furrow. Epimeral areas of segment of leg 2 rather pointed posteriorly; those of segments of legs 1, 3, and 4 rounded.

Segment of leg 5 (Pl. 6, fig. 50) 88 × 146 μ. Between this segment and genital segment a short intersegmental sclerite ventrally. Genital segment a little longer than wide, 177 μ in length, 159 μ in width in its anterior two-thirds, and 114 μ in width in its constricted posterior third, and showing a slight middorsal hump anteriorly. Areas of attachment of egg sacs situated dorsolaterally on anterior part of posterior third; each area (Pl. 6, fig. 50) with 2 setae (outer 77 μ long and naked, inner 23 μ and feathered) and between them a small spinous process 6 μ long. Posterior margin of genital segment with a membrane which simulates spinules laterally. Two postgenital segments 52 × 95 and 34 × 88 μ respectively.

Caudal ramus (Pl. 7, fig. 51), inserted ventrally on anal segment, a little wider than long, 28 × 35 μ, taking average length as 28 μ, the ramus being longer ventrally (31 μ) than dorsally (25 μ). Long naked setule on outer margin 31 μ long. Outer lateral seta 120 μ and naked. Outermost terminal seta 180 μ with lateral spinules. Innermost terminal seta long, 451 μ, and naked. Two long median terminal setae 460 μ (outer) and 660 μ (inner), both with lateral spinules and their "pegged" regions punctate. These 2 setae inserted between ventral flap (with rows of spinules) and dorsal flap of form shown in figure and bearing very small spinules near pedicellate dorsal seta (33 μ long and naked). Group of 2–3 minute hairs on dorsal surface of ramus.

Dorsal surface of prosome with only a few hairs. Dorsal surface of urosome with more abundant hairs as in Pl. 6, fig. 50; ventral surface with very few hairs. Ratio of length of prosome to that of urosome 2·45 : 1.

Egg sac (Pl. 6, fig. 49) elongated and rather stout, about 810 × 300 μ, more than twice as long as the urosome, and containing many eggs about 52 μ in diameter.

Rostral area (Pl. 7, fig. 52) rather pointed.

First antenna with armature as in *S. kossmanni* and *S. affinis*. All setae apparently naked. Lengths of segments (measured as before) 30 (67 μ along anterior edge), 107, 29, 53, 46, 23, and 15 μ respectively. Terminal aesthete and adjacent seta with common base. Sclerite on ventral surface of third segment. Long terminal seta 234 μ in length, distinctly less than length of antenna (340 μ).

Second antenna (Pl. 7, fig. 53) 3-segmented, third segment showing no evidence of division. Armature 1; 1; 3 + 5 + 1 claw, as in 2 previous species. Seta on segment 1 unusually long (165 μ) and setose. Seta on segment 2 relatively short (44 μ) and naked. Claw 68 μ along its axis. On anterior surface near base of claw a short vermiform protrusion (aesthete ?). Anterior surface of second antenna pilose as in figure.

Labrum (Pl. 7, fig. 54) with attenuated unornamented lobes.

Mandible (Pl. 7, fig. 55) with elements of outer row beginning as stout spines and diminishing to slender spinules; first element in inner row not much larger than rest; a patch of spinules on posterior proximal surface of mandible. Paragnath a small lobe as in *S. affinis*. First maxilla with 4 elements as in 2 previous species, but ornamented spiniform element only very finely spinulose. Second maxilla (Pl. 7, fig. 56) with first segment ornamented with a few spinules on both anterior and posterior surfaces and with its proximal ventral margin angularly produced. Second segment with postero-inner finely barbed seta, long inner spiniform seta with its posterior surface spinulose but anterior surface smooth, and with terminal spiniform process spinulose and showing 2 prominent spines near base. Maxilliped (Pl. 7, fig. 57) with first segment unarmed, second with usual 2 setae and with spinules as in figure, and third with 2 setae (one spinulose, other naked) and terminal spiniform process.

Area between maxillipeds and first pair of legs not protuberant and resembling that in *S. kossmanni*.

Rami of legs 1–4 like those in 2 previous species, with same spine and setal formula. Fine ornamentation much like that in *S. kossmanni*. Last segment of endopod of leg 2 without a bifurcated spinous process (Pl. 7, fig. 58), and having a form somewhat different from that in *S. kossmanni*. Last segment of endopod of leg 3 (Pl. 7, fig. 59) of a form slightly different from *S. kossmanni*. Leg 4 (Pl. 7, fig. 60) with inner seta on coxa relatively short (26 μ) and naked. Slightly barbed inner seta on second segment of exopod shorter than setae on third segment, recurved, and lying (in alcoholized specimens) over the posterior surface of ramus. Endopod (Pl. 8, fig. 61) with 2 segments clearly separated. First segment 31 × 28 μ, with inner seta 58 μ long and feathered. Second segment 69 μ long, 28 μ in greatest width, and 18 μ wide at narrowest point, its feathered inner seta 74 μ, inner terminal spine 76 μ with a very narrow lamella along one edge, and outer terminal spine 55 μ with finely serrated lamellae and with a delicately trifurcate tip. Row of hairs on outer margin of this segment interrupted at slight indentation.

Leg 5 (Pl. 8, fig. 62) with free segment swollen on inner margin, its greatest dimensions 39 × 19 μ. Two terminal naked setae extremely unequal, inner 34 μ, outer 170 μ. Seta on body near insertion of free segment about 35 μ and feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 6, fig. 50).

Colour in life in transmitted light translucent to grayish, eye red, egg sacs gray.

MALE. Body (Pl. 8, fig. 63) with prosome more slender than in female. Length (without ramal setae) 0·73 mm. (0·72–0·73 mm.) and greatest width 0·29 mm. (0·28–0·29 mm.), based on 3 specimens (allotype, 1 paratype, and 1 specimen collected 14th December, 1963). Ratio of length to width of prosome 1·62 : 1.

Segment of leg 5 (Pl. 8, fig. 64) 46 × 79 μ. Ventral intersegmental sclerite absent. Genital segment a little longer than wide, 125 × 104 μ, with sides in dorsal view nearly parallel. Three postgenital segments 42 × 69, 33 × 55, and 20 × 53 μ from anterior to posterior.

Caudal ramus like that of female. Surfaces of prosome and urosome, as in female, sparsely ornamented with hairs. Ratio of length of prosome to that of urosome 1·70 : 1.

Rostral area, first antenna, second antenna, labrum, mandible, paragnath, and first maxilla resembling those in female. Second maxilla much like that of female, with same process on first segment, but with long inner seta less strongly developed and with terminal spiniform process weaker and showing near base only 1 prominent spine, the second being greatly reduced in size. Maxilliped (Pl. 8, fig. 65) slender. Spinules on second segment arranged differently than in 2 previous species. Claw 117 μ long (measured along its axis) and showing 2 slight flexures, with only indication of division being an interruption in fringe of delicate hyaline spinules along concave margin. Two setae near base of claw 67 μ (with a few barbs near tip) and 8 μ (naked).

Area between maxillipeds and first pair of legs resembling that of female.

Legs 1–4 resembling those of female, with same spine and setal formula.

Leg 5 (Pl. 8, fig. 66) with free segment lacking inner swelling, 18 × 9 μ. Two terminal setae 20 μ (inner) and 58 μ (outer), ratio between them being 2·9 : 1, instead of 7 : 1 as in female. Seta on body near insertion of free segment about 20 μ long and slightly feathered.

Leg 6 (see Pl. 8, fig. 64) resembling that of *S. kossmanni*, with a minute spinous process and 2 unequal setae, one naked (64 μ), other feathered (20 μ).

Spermatophores not observed.

Colour in life in transmitted light as in female.

(The specific name *longiseta*, Latin = long seta, alludes to the unusually long terminal seta on the fifth leg in the female).

COMPARISON WITH RELATED SPECIES. From the four species of *Stellicola* known to have two postgenital segments in the female, *S. longiseta* may readily be separated by its very long seta on leg 5. In addition, this species from *Mithrodia* has a caudal ramus which is a little wider than long, instead of 4 : 1 as in *S. gracilis* (Thompson & A. Scott, 1903), about 2 : 1 as in *S. lankensis* (Thompson & A. Scott, 1903), and 6·3 : 1 or 7 : 1 as in *S. affinis*. The female of the species from Madagascar whose description by Humes and Ho is in press, although having a nearly quadrate caudal ramus, differs from *S. longiseta* in having a rounded rostrum, in the seta on the first segment of the second antenna being not unusually long, in the two setae on the endopod of leg 4 being finely barbed instead of feathered, in the two terminal setae on leg 5 having a ratio of 3 : 1 instead of 7 : 1, and in the ratio of the length of the prosome to that of the urosome being 2·0 : 1 instead of 2·45 : 1. In the male, the species of Humes and Ho differs from *S. longiseta* in having the genital segment somewhat tapered anteriorly instead of having nearly parallel sides, and in the claw of the maxilliped being evenly recurved instead of showing two flexures.

From all four of these species *S. longiseta* may be further distinguished by details in ornamentation of the appendages.

S. longiseta appears to be closest to the species to be described by Humes and Ho, both having a very short caudal ramus and a somewhat similar genital segment in the female.

Stellicola femineus n. sp.

Pl. 8, fig. 67; Pl. 9, figs. 68–75; Pl. 10, figs. 76–84; Pl. 11, figs. 85–92

TYPE MATERIAL. 8 ♀, 9 ♂, and 1 copepodid from 1 starfish, *Leiaster leachi* Gray, in a depth of 0·5 m., Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected 8th August, 1960. Holotype female, allotype, and 11 paratypes (5 ♀, 6 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.10–12, and the remaining paratypes in the collection of A. G. Humes.

Other specimens. 4 ♀, 9 ♂ from 1 starfish, *Leiaster speciosus* von Martens, in 0·5 m., Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar, 2nd October, 1960.

FEMALE. Body (Pl. 8, fig. 67) with broad flattened prosome. Length (not including setae on caudal rami) 1·41 mm. (1·32–1·49 mm.) and greatest width 0·94 mm. (0·88–0·99 mm.), based on 10 specimens (holotype, 7 paratypes, and 2 specimens from *Leiaster speciosus*). Ratio of length to width of prosome 1·06 : 1. Segment of leg 1 completely fused with head. Epimeral areas of segments of legs 1 and 2 pointed posteriorly; those of segment of leg 3 also pointed but indented as in figure. Segment of leg 4 small, with its tergum and rounded epimeral areas partly overlapped by preceding segment.

Segment of leg 5 (Pl. 9, fig. 68) 164 × 257 μ. Intersegmental sclerite not evident. Genital segment broad and flattened, 135 × 239 μ, wider than long, with expanded rounded lateral margins. Areas of attachment of egg sacs located posteriorly and slightly dorsally; each area (Pl. 9, fig. 69) with 2 unequal feathered setae 34 and 17 μ in length, each arising from a pedicel. Three postgenital segments 44 × 99, 39 × 89, and 59 × 77 μ from anterior to posterior.

Caudal ramus (Pl. 9, fig. 70), inserted slightly ventrally, subquadrate, 30 × 33 μ, a little wider than long. Long naked setule (55 μ) midway on outer margin. Pedicellate dorsal seta 60 μ and feathered. Outer lateral seta 101 μ and naked, inserted close to outermost terminal seta (208 μ with straight lateral spinules). Innermost terminal seta 234 μ with straight lateral spinules. Two long terminal setae, inserted between dorsal (smooth) and ventral (with row of minute spinules) flaps, 396 μ (outer) and 540 μ (inner) and both with unusually long hairlike recurved lateral spinules.

Dorsal surface of prosome with short hairs. Dorsal and ventral surfaces of urosome with many hairs as shown in Pl. 9, fig. 68. Ratio of length of prosome to that of urosome 2·32 : 1.

Egg sac (see Pl. 8, fig. 67) moderately elongated and stout, 682 × 341 μ, extending far beyond ends of caudal rami, and containing many eggs about 70 μ in diameter.

Rostral area (Pl. 9, fig. 71) prominent, its posterior margin a little truncated.

First antenna (Pl. 9, fig. 72) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 46 (35 μ along anterior margin), 107, 34, 36, 25, 13, and 12 μ respectively. Formula for armature as in 3 previous species. Certain setae with short hairs as in figure. Ventral sclerite on third segment. Long terminal seta 203 μ in length, distinctly less than length of antenna (270 μ).

Second antenna (Pl. 9, fig. 73) 3-segmented, 495 μ in length, with no evidence of division in segment 3. Armature 1; 1; 3 + 5 + 1 claw as in 3 previous species. Third segment elongated, 300 μ along outer edge, 187 μ along inner edge, with a sclerotized strongly bent pointed process near base of claw (Pl. 9, fig. 74). Claw 96 μ along its axis. All setae naked.

Labrum (Pl. 9, fig. 75) with moderately rounded unornamented lobes.

Mandible (Pl. 10, fig. 76) in general resembling that of *S. longiseta* but without proximal patch of spinules. Paragnath (see Pl. 9, fig. 71) a small lobe. First maxilla (Pl. 10, fig. 77) with 4 elements. Second maxilla (Pl. 10, fig. 78) showing second segment with long inner spiniform seta bearing a row of spinules, those in middle of row much longer and stronger; terminal spiniform process with a single large tooth-like proximal spine (2 such spines seen on left second maxilla in 1 female). Maxilliped (Pl. 10, fig. 79) with first segment having a distal patch of spinules, second with 1 naked and 1 feathered seta and rows of spinules as in figure, and third with 2 small unequal setae and terminal spiniform process.

Area between maxillipeds and first pair of legs not protuberant and formed as in Pl. 9, fig. 71.

Rami of legs 1–4 (Pl. 10, figs. 80, 81, 82, and 83) like those in 3 previous species with same spine and setal formula. Endopods of legs 1–3 rather elongated; last segment of endopod of leg 2 without a bifurcated spinous process. In leg 4 coxa with inner seta apparently reduced to a mere vestige. Feathered inner seta on second segment of exopod short and lying free of ramus. Endopod (Pl. 10, fig. 84) slender, 2 segments clearly separated. First segment 38 × 15·5 μ with its inner seta short, 30 μ, and finely barbed distally. Second segment 50 × 12 μ (greatest dimensions), its feathered inner seta 52 μ, inner terminal spine 76 μ, and outer terminal spine 31 μ, both spines finely barbed. (In another female first segment 33 × 20 μ, and second segment 58 × 14·5 μ). Marginal hairs on segments as in figure.

Leg 5 (Pl. 11, fig. 85) with elongated slightly recurved slender free segment, 71 × 22 μ (greatest dimensions), tapering slightly distally. Two terminal setae naked and very unequal, inner 22 μ, outer 113 μ. Seta on body near insertion of free segment about 48 μ and feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 9, fig. 69).

Colour in life in transmitted light orange-red to deep red, eye red, egg sacs red.

Male. Body (Pl. 11, fig. 86) with broad flattened prosome as in female. Length (excluding setae on caudal rami) 0·85 mm. (0·82–0·88 mm.) and greatest width 0·48 mm. (0·46–0·49 mm.), based on 10 specimens (allotype, 8 paratypes, and 1 specimen from *Leiaster speciosus*). Ratio of length to width of prosome 1·11 : 1.

Segment of leg 5 completely fused dorsally with genital segment (Pl. 11, fig. 87), and only a faint indication of separation between these 2 segments ventrally; segment of leg 5 and genital segment combined a little longer than wide, 221 × 195 μ. No intersegmental sclerite. Four postgenital segments 28 × 68, 27 × 62, 24 × 57, and 29 × 52 μ, from anterior to posterior.

Caudal ramus similar to that of female but smaller, 18 × 21 μ.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 1·73 : 1.

Rostral area, first antenna, and second antenna as in female. Labrum (Pl. 11, fig. 88) with 2 lobes apparently somewhat more pointed than in female. Mandible, paragnath, first maxilla, and second maxilla like those of female. Maxilliped (Pl. 11, fig. 89) without long terminal claw, but instead having a form rather like that of female. First segment without ornamentation, second with 2 small naked setae (one hyaline and with a blunt tip) and bearing a patch of spinules, and third with one of 2 setae at base of naked terminal spiniform process greatly elongated.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 resembling in major features those of female, having same spine and setal formula. In legs 2 and 3 apparently a slight sexual dimorphism in lengths of 3 spines on last segment of endopod (from proximal to distal in leg 2 of male 12, 13, and 24 μ, but in female 22, 21, and 34 μ; in leg 3 of male 12, 13, and 25 μ, but in female 23, 24, and 40 μ). Dimensions of endopod of leg 4: first segment 22 × 13 μ, with its seta 21 μ; second segment 31 × 11 μ, with its seta 34 μ and spines 50 μ (inner) and 24 μ (outer).

Leg 5 (Pl. 11, fig. 90) with rectangular free segment relatively shorter than in female, 19 × 9 μ, with 2 terminal setae 16 μ (inner) and 56 μ (outer), with ratio of 3·5 : 1, instead of 5 : 1 as in female. Seta on body near insertion of free segment about 22 μ long and feathered.

Leg 6 (Pl. 11, fig. 91) consisting of a posterolateral flap on ventral surface of genital segment and bearing at either side of a small spinous process 2 slender naked setae 46 and 29 μ long.

Spermatophore, observed only inside body of male, of elongated form (Pl. 11, fig. 92).

Colour in life in transmitted light paler orange-red than in female, eye red.

(The specific name *femineus*, Latin = womanly or feminine, alludes to the weakly prehensile, female-like maxilliped in the male of this species).

COMPARISON WITH RELATED SPECIES. The female of S. *femineus* differs from almost all other known species in the genus in having the free segment of leg 5 at least three times longer than wide. The only species which has similar proportions in leg 5 is the species of Humes and Ho (in press) where the free segment is 65 × 21 μ. In this species, however, there are only two postgenital segments in the female.

The male of S. *femineus* is unique in the genus in having a female-like maxilliped, without a well-formed prehensile claw.

Stellicola pollex n. sp.

Pl. 11, fig. 93; Pl. 12, figs. 94–101; Pl. 13, figs. 102–109; Pl. 14, figs. 110–114.

TYPE MATERIAL. 5 ♀ and 4 ♂ from 2 starfishes, *Linckia laevigata* (L.), in a depth of 10 m., at Nosy Ovy (=Berafia), 13° 59′ S, 47° 46′ 30″ E, to the southwest of Nosy Bé, Madagascar. Collected 1st October, 1964. Holotype, allotype, and 5 paratypes (3 ♀, 2 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.13–15, and the remaining 2 paratypes (dissected) in the collection of A. G. Humes.

FEMALE. Body (Pl. 11, fig. 93) with broad flat prosome. Length (without setae on caudal rami) 0·99 mm. (0·94–1·03 mm.) and greatest width 0·78 mm. (0·68–0·88 mm.), based on 5 specimens. Ratio of length to width of prosome 0·95 : 1, prosome being slightly wider than long. Segment of leg 1 separated dorsally and laterally from head by a distinct furrow. Epimera of metasomal segments as in *S. femineus*.

Segment of leg 5 (Pl. 12, fig. 94) 91 × 180 μ. Ventrally between this segment and genital segment a very short intersegmental sclerite. Genital segment broad and flattened, 161 × 198 μ, wider than long, with expanded rounded lateral margins lobed posteriorly. Areas of attachment of egg sacs located ventrally and hidden in dorsal view by the lobes; each area (Pl. 12, fig. 95) with 2 naked setae, 39 and 35 μ in length, borne on pedicels. Three postgenital segments 35 × 64, 36 × 62, and 34 × 57 μ from anterior to posterior.

Caudal ramus (Pl. 12, fig. 96), inserted ventrally, quadrate, 20 × 20 μ, with naked setule on outer margin 19 μ long. Pedicellate dorsal seta 36 μ and feathered. Outer lateral seta 60 μ and naked. Outermost terminal seta 127 μ and innermost 96 μ, both with lateral spinules. Two long terminal setae, inserted between flaps as in *S. femineus*, 320 μ (outer) and 495 μ (inner), both with short spinules.

Dorsal surface of prosome with scattered hairs (not shown in Pl. 11, fig. 93, because of the reduced scale). Dorsal surface of urosome with hairs and refractile points as in Pl. 12, fig. 94; ventral surface with very little ornamentation. Ratio of length of prosome to that of urosome 2·5 : 1.

Egg sacs not present on any of females collected.

Rostral area as in *S. femineus*, though posterior margin less truncated.

First antenna (Pl. 12, fig. 97) more slender than in *S. femineus*, but with same segmentation and armature. Lengths of segments (measured as before) 44 (35 μ along anterior margin), 116, 45, 50, 33, 20, and 16 μ respectively. One seta on segment 6 and 4 setae on segment 7 with lateral hairs; rest of setae naked. Terminal seta 117 μ, about one-third length of antenna (330 μ).

Second antenna (Pl. 12, fig. 98) slender as in *S. femineus*, with third segment showing no indication of division. Armature 1; 1; 3 + 5 + 1 claw as in 4 previous species. Near base of claw a small spinous process. Claw 61 μ along its axis. All setae naked.

Labrum as in *S. femineus*, though lobes a little more rounded.

Mandible (Pl. 12, fig. 99) with slender spinules along outer margin and row of dentiform spinules along inner margin (proximal spinule enlarged and preceded by a slight flange). Paragnath (Pl. 12, fig. 100) a small lobe with very slender spinules. First maxilla in general like that of *S. femineus*. Second maxilla (Pl. 12, fig. 101) with first segment unarmed, second with 2 postero-inner elements (a slender barbed seta and a long spiniform seta ornamented with a row of spinules along its distal edge and showing a very weak line of division proximally) and terminating in a spiniform process bearing rows of teeth as in figure. Maxilliped (Pl. 13, fig. 102) resembling in major features that of *S. femineus*, though details of ornamentation somewhat different.

Area between maxillipeds and first pair of legs as in *S. femineus*.

Rami of legs 1–4 (Pl. 13, figs. 103, 104, 105, and 106) segmented as in previous 4 species, with similar spine and setal formula, except for endopod of leg 4 which is 0–0 ; II. Endopods of legs 1–3 rather elongated as in *S. femineus ;* last segment of endopod of leg 2 without a bifurcated spinous process. Leg 4 with only a vestige of inner coxal seta. Inner seta on second segment of exopod short (22 μ) and apparently naked. Endopod (Pl. 13, fig. 107) 41 × 10 μ, only incompletely divided into 2 segments, its inner margin entire. Two inner setae usually seen in *Stellicola* here absent, and only armature of endopod consisting of 2 terminal smooth spines 60 μ (inner) and 31 μ (outer) in length. Rows of hairs along outer and inner margins of endopod, outer row interrupted at incomplete division of ramus.

Leg 5 (Pl. 13, fig. 108) with free segment 55 × 27 μ (greatest dimensions, its inner proximal margin somewhat irregular and produced). Two terminal setae naked and unequal, inner 43 μ, outer 56 μ. Seta on body near insertion of free segment about 37 μ and slightly feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 12, fig. 95).

Colour in life in transmitted light slightly opaque, eye red, egg sacs gray.

MALE. Body (Pl. 13, fig. 109) resembling that of female. Length (excluding setae on caudal ramus) 0·55 mm. (0·53–0·56 mm.) and greatest width 0·36 mm. (0·35–0·37 mm.), based on 4 specimens. Ratio of length to width of prosome 1·07 : 1.

Segment of leg 5 and genital segment fused (Pl. 14, fig. 110) as in *S. femineus ;* these fused segments 127 μ long, 115 μ wide just in front of leg 5, and 105 μ wide behind leg 5. No intersegmental sclerite. Four postgenital segments 28 × 46, 23 × 43, 22 × 40, and 18 × 36 μ from anterior to posterior.

Caudal ramus similar to that of female but smaller, 12·5 × 13 μ.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 2·07 : 1.

Rostral area and first antenna as in female. Second antenna also resembling that of female, but having a conspicuous thumb-like process on inner margin of third segment (Pl. 14, fig. 111). Labrum, mandible, paragnath, first maxilla, and second maxilla like those in female. Maxilliped (Pl. 14, fig. 112) slender, with long terminal claw. First segment unarmed, second with 2 naked setae and 2 patches of spinules, third short and unarmed. Proximal half of claw probably representing fourth segment. Claw only slightly recurved, 130 μ in length along its axis, showing faint indication of division about midway, with a fringe of small spinules along its concave margin and 2 unequal setae 8 μ (naked) and 26 μ (slightly barbed) near its base.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 resembling those of female, with same spine and setal formula. As in *S. femineus* a slight sexual dimorphism in lengths of 3 spines on last segment of endopod of legs 2 and 3 (from proximal to distal in leg 2 of male 9, 10, and 22 μ, but in female 16·5, 17·5, and 35 μ; in leg 3 of male 8, 10, and 20 μ, but in female 16·5, 18·5, and 35 μ). Dimensions of endopod of fourth leg 22 × 8 μ, with inner spine 31 μ and outer spine 17 μ.

Leg 5 (Pl. 14, fig. 113) with free segment smaller and having nearly parallel sides, 20 × 8 μ, the terminal setae 18 μ (inner) and 52 μ (outer), with ratio of 2·9 : 1, instead of 1·3 : 1 as in female.

Leg 6 (Pl. 14, fig. 114) consisting of a posterolateral flap on ventral surface of genital segment and bearing 2 slender naked setae 21 and 36 μ.

Spermatophores not observed.

Colour in life in transmitted light as in female.

(The specific name *pollex*, Latin = a thumb, refers to the thumb-like process on the third segment of the second antenna of the male).

COMPARISON WITH OTHER SPECIES. *S. pollex* has two readily observable characters by which it may be distinguished from all other species in the genus, namely, the thumb-like process on the third segment of the second antenna in the male and the armature of the endopod of leg 4 (0–0; II) in both sexes.

In the fifteen previously known species and in the four species described above the formula for the endopod of leg 4 is 0–1; II, 1. Such an armature seems to be a stable and constant feature in the genus. The unusual armature in *S. pollex* might suggest at first glance that this species should be removed to a separate genus. However, other features of *S. pollex* (first antenna, second antenna, mouthparts, legs 1–5, and body form) conform very closely to the pattern of *Stellicola*. The structure of the mandible (which is an important generic character in the Lichomolgidae) is very much like that in other species of the genus. Therefore, in spite of the rather remarkable difference in the armature of this endopod, we are considering the species to belong to *Stellicola*.

Stellicola oreastriphilus Kossmann, 1877

Pl. 14, figs. 115–120

Two females and one male were recovered from washings of a single starfish, *Protoreaster nodosus* (L.), in a depth of 2 m., on *Cymodocea*, at Ambatoloaka, Nosy Bé, 15th October, 1960. This represents a new host record, the species having been previously found on six other starfishes—*Asterope carinifera* (Lamarck) in the Red Sea by Kossmann (1877), on *Protoreaster lincki* (Blainville), *Culcita schmideliana* (Retzius), *Pentaceraster mammillatus* (Audouin), and *Poraster superbus* (Möbius) in Madagascar by Humes & Cressey (1961), and on *Choriaster granulatus* (Lütken) in Madagascar by Humes & Ho (in press).

In connection with the description of the five new species above, specimens of *S. oreastriphilus* (from a lot of approximately 1,000 individuals washed from 200 *Protoreaster lincki*, in a depth of 10 cm., at Pte. Mahatsinjo, Nosy Bé, 6th September, 1964) were restudied. The dissections were done in lactic acid (see Humes & Gooding, 1964), enabling us to see certain details not easily observed in the original dissections in glycerine. Notes on these features are offered here as a supplement to the work of Humes & Cressey (1961).

FEMALE. The flattened genital segment (Pl. 14, fig. 115) expanded laterally, with subparallel lateral margins. A pair of ventral refractile sclerotizations present on sides of segment. Tip of second antenna (Pl. 14, fig. 116) bearing 5 setae and 1 claw. Paragnath (Pl. 14, fig. 117) a hairy lobe bearing a sclerotized process. Maxilliped (Pl. 14, fig. 118) with second segment having 2 setae (one surficial, other on a hyaline base at inner marginal angle) and a crescentic row of spinules ; third segment with 2 very unequal small setae at base of terminal spiniform process. Endopod of leg 4 (Pl. 14, fig. 119) with marginal hairs as in figure.

MALE. Segment of leg 5 and genital segment (Pl. 14, fig. 120) fused completely dorsally and their ventral separation suggested by a very indistinct line. Fused segments 120 μ long, 109 μ wide just in front of leg 5, and 101 μ wide posterior to leg 5. (The rather distinct separation of the two segments shown by Humes & Cressey, 1961, fig. 25, is not present in the material which we have re-examined).

Stellicola caeruleus (Stebbing, 1900)

Pl. 15, figs. 121–128 ; Pl. 16, figs. 129–134 ; Pl. 17, figs. 135–141

This species was placed by Stebbing (1900, pp. 664–666, plate LXXIVB) in a new genus *Linckiomolgus*, but, as Stock (1957) has pointed out, and as will be seen from the redescription below, it belongs more properly to *Stellicola*.

Through the kindness of Miss Patricia D. Lofthouse we have been able to study syntypes (1 female and 1 male) of *S. caeruleus* [Brit. Mus. (Nat. Hist.) reg. no. 1928.12.1.3020]. These are labelled " China Sea on blue *Linckia* ", though the type locality given by Stebbing was Feather Island, China Straits, New Guinea. The dissections of these specimens, mounted on two slides, have been returned to the British Museum (Nat. Hist.). Although the condition of the specimens (which were in amplexus) was less than perfect, with certain setae broken or missing, the major features could be observed in the dissections. Stebbing's original description being inadequate in many respects, especially regarding the mouthparts, a redescription of the species based on syntypic material is desirable.

FEMALE. Body (Pl. 15, fig. 121) with greatly expanded prosome. Length (without setae on caudal rami) 1·23 mm. and greatest width 0·88 mm. Ratio of length to width of prosome 0·97 : 1, being a little wider than long. Segment of leg 1 completely fused with head. Epimeral areas of metasomal segments resembling those of *S. femineus*.

Genital segment (Pl. 15, fig. 122) wider than long, 156 × 208 μ, broadly rounded laterally in its anterior half and tapering in its posterior half where the areas of attachment of the egg sacs are located laterally. Dorsally with two longitudinal posterior elevations with sclerotization as in figure. Each egg sac attachment area with 2 unequal setae, one arising from a prominent slender pedicel 31 × 8 μ. Three postgenital segments 60 × 86, 42 × 78, and 52 × 72 μ from anterior to posterior.

Caudal ramus (Pl. 15, fig. 123) only a little longer than wide, 32 × 28 μ.

Ratio of length of prosome to that of urosome 2·32 : 1.

Egg sac broken on female examined; an isolated egg about 74 μ in diameter.

Rostral area (Pl. 15, fig. 124) incomplete posteriorly.

First antenna (Pl. 15, fig. 125) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 55 (44 μ along anterior margin), 113, 39, 43, 33, 15, and 14 μ respectively. Formula for armature 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in all 5 new species described above and as in *S. oreastriphilus*. Ventral sclerite present on third segment.

Second antenna (Pl. 15, fig. 126) with a single claw 79 μ along its axis and with armature as in *S. femineus*. Third segment 166 μ along outer side, 91 μ along inner side, with no evidence of division.

Labrum as in Pl. 15, fig. 124.

Mandible (Pl. 15, fig. 127) with first 2 elements of inner row only slightly larger than succeeding ones. Paragnath a small lobe with coarse hairs. First maxilla with 4 elements. Second maxilla (Pl. 15, fig. 128) with second segment with long inner spiniform seta bearing a row of spinules, those in middle of row somewhat longer; terminal spiniform process with strong graduated teeth. Maxilliped (Pl. 16, fig. 129) 3-segmented, with second segment apparently having only 1 seta, and with 2 very unequal spinules near base of short terminal claw-like process.

Area between maxillipeds and first pair of legs resembling that of *S. femineus*.

Rami of legs 1–4 (Pl. 16, figs. 130, 131, 132, and 133) segmented and armed as in *S. kossmanni*, *S. affinis*, *S. longiseta*, and *S. femineus*, except for last segment of exopod of leg 3 which has formula of II, I, 5. In leg 4 coxa with only a minute knob probably representing a vestige of inner coxal seta seen in other species. Inner seta on second segment of exopod 25 μ long and naked. Endopod 2-segmented, 2 segments distinctly separated. First segment 27 × 15 μ, with its inner seta 36 μ and finely barbed. Second segment 31 × 12 μ, its inner seta 42 μ and feathered, inner terminal spine 66 μ and barbed, outer spine 29 μ with only a few minute barbs. (Marginal hairs on endopod segments not discernible).

Leg 5 (Pl. 16, fig. 134) with free segment about 44 × 17 μ, bearing 2 very unequal terminal setae.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 15, fig. 122).

MALE. Body (Pl. 17, fig. 135) with prosome somewhat less expanded than in female. Length (excluding ramal setae) 0·52 mm. and greatest width 0·32 mm. Ratio of length to width of prosome 1·09 : 1, being a little longer than wide.

Segment of leg 5 fused with genital segment (Pl. 17, fig. 136), as in *S. femineus*, *S. pollex*, and *S. oreastriphilus*. These 2 segments combined longer than wide: 110 μ in length, 83 μ wide at level of fifth legs, and 75 μ wide posterior to these legs, where lateral margins are subparallel. Four postgenital segments 30 × 47, 30 × 44, 20 × 40, and 22 × 37 μ from anterior to posterior.

Caudal ramus similar to that of female but smaller, 19 × 15 μ.

Ratio of length of prosome to that of urosome 2·05 : 1.

Rostral area (Pl. 17, fig. 137) well-defined posteriorly, with its border there slightly indented.

First antenna, second antenna, labrum, mandible, paragnath, and first maxilla like those of female. Second maxilla (Pl. 17, fig. 138) with second segment much like that of female, but with first segment showing 3 peculiar sclerotized processes arising ventrally. (Possibly these are adhesive pads). Maxilliped (Pl. 17, fig. 139) small, 2-segmented, with terminal claw 22 μ along its axis. Both segments without ornamentation or armature ; a small knob on basal area of claw.

Legs 1–4 like those in female, with same spine and seta formula.

Leg 5 (Pl. 17, fig. 140) with a small free segment, 12 × 7 μ, bearing 2 terminal setae 18 μ (inner) and 55 μ (outer).

Leg 6 (Pl. 17, fig. 141) consisting of the usual posterolateral flap on ventral surface of genital segment and bearing 2 unequal setae.

Spermatophores not observed.

COMPARISON WITH OTHER SPECIES. Based on our study of syntypes, *S. caeruleus* shows three features not found in the other nineteen species of the genus, as far as known : the two posterior sclerotized elevations on the dorsal surface of the genital segment of the female, the three peculiar sclerotized processes on the first segment of the second maxilla in the male, and the formula of II, I, 5 on the last segment of the exopod of leg 3 in both sexes. A small 2-segmented maxilliped with a short claw is also found in the male of *S. holothuriae* (Ummerkutty), but this Indian species differs from *S. caeruleus* in having the formula III, I, 5 on the last segment of the exopod in leg 3 and in the shape of the caudal ramus (much wider than long). *S. caeruleus* may thus readily be distinguished from other members of the genus.

NOTES ON THE VARIABILITY OF CERTAIN FEATURES IN THE GENUS *STELLICOLA*

The twenty species here recognized in the genus *Stellicola* exhibit certain variations in external structure worthy of note. The second antenna may bear terminally a single claw, two claws, or three claws. Those with three claws are the four West African species : *S. frequens*, *S. astropectinis*, *S. luidiae*, and *S. lautus*. (In all of these the middle spine on the last segment of the endopod of leg 2 is unusually short, whereas in other species, as far as known, this spine is not thus shortened ; the second segment of the endopod of leg 4 has a sharp spinous process midway on its outer margin opposite the inner seta). The only species with two claws is *S. clausi*. The remaining fifteen species have a single claw. The third segment of the second antenna in some species may show an incomplete division (as in the species to be described by Humes and Ho, in press, and in *S. kossmanni*).

The armature of legs 1–4 is similar in all species (where it has been described) except for *S. caeruleus*, where the formula for the last segment of the exopod of leg 3 is II, I, 5, and *S. pollex*, where the endopod of leg 4 has a formula of 0–0 ; II.

In a few species the basis of leg 4 is greatly elongated and the inner coxal seta is absent, this seta being perhaps represented by a small knob, as in *S. femineus*, *S. pollex*, and *S. caeruleus*. *S. thorelli*, *S. pleurobranchi*, *S. curticaudatus*, *S. longicaudatus*, and *S. holothuriae* appear to be similarly constructed, but the exact nature of the protopodal segments of leg 4 is impossible to determine from the descriptions and figures of these species. *S. oreastriphilus* represents an intermediate form between those species with an elongated basis and those with a short basis (as in *S. kossmanni*, for example).

The maxilliped of the male in most species is elongated and bears a long prehensile claw, but in *S. femineus* it is female-like and only weakly prehensile, and in *S. caeruleus* it is small, 2-segmented, with a short claw.

The second maxilla of the male of *S. caeruleus* is remarkable in the development of three peculiar sclerotized processes on the first segment. In most other species, as far as known, there is no sexual dimorphism in this appendage, but in *S. longiseta* and *S. affinis* the second maxilla of the male shows slight differences from that of the female.

In the males of certain species the segment of leg 5 and the genital segment are almost completely fused, as in *S. oreastriphilus*, *S. femineus*, *S. pollex*, and *S. caeruleus*. It may be noted that the tendency in leg 4 toward elongation of the basis and loss of the inner coxal seta occurs in the same four species.

The males of five species (*S. thorelli*, *S. pleurobranchi*, *S. lankensis*, *S. curticaudatus*, and *S. longicaudatus*) are unknown, and the available descriptions of the females are lacking in detail. Hence, it is impossible at present to determine whether or not these variations exist in them.

The significance of such variations as mentioned above is not clear. The four West African species seem to be closely related and set apart from the rest, perhaps constituting an evolutionary line within the genus. It will be necessary, however, to have much more information on the species within the genus before well-founded conclusions regarding evolutionary relationships can be made. Undoubtedly many more species of *Stellicola* remain to be discovered, since relatively few species of potential asteroid hosts have been examined.

KEYS TO THE SPECIES OF *STELLICOLA*

The preparation of keys for the identification of the species of *Stellicola* presents certain difficulties, since detailed information regarding various structures in several species is not available in the existing descriptions or figures. Furthermore, the males of five species (*thorelli*, *pleurobranchi*, *lankensis*, *curticaudatus*, and *longicaudatus*) are unknown and consequently cannot be included in the key. The keys given here are entirely artificial and are presented only as aids in identification. Final determination of a species should be made by reference to the original descriptions and figures, or to actual specimens, if available.

FEMALES

1	Two postgenital segments	2
	Three postgenital segments	6
2	Caudal ramus 2 × or more than 2 × longer than wide	3
	Caudal ramus short, nearly quadrate	5

3 Caudal ramus at least 4× longer than wide 4
Caudal ramus about 2× longer than wide . . . . ***lankensis***
4 Caudal ramus 6·3–7× longer than wide . . . . ***affinis***
Caudal ramus 4× longer than wide . . . . ***gracilis***
5 Seta on first segment of second antenna unusually long, reaching nearly to end of appendage ; free segment of leg 5 swollen on inner margin ; caudal ramus slightly wider than long, 28 × 35 μ . . . . ***longiseta***
Seta on first segment of second antenna not unusually long ; free segment of leg 5 with sides nearly parallel ; caudal ramus slightly longer than wide, 28 × 23 μ species of Humes and Ho, in press
6 With more than 1 claw on last segment of second antenna 7
With only 1 claw on last segment of second antenna 11
7 With 3 claws on last segment of second antenna 8
With 2 claws on last segment of second antenna . . . . ***clausi***
8 Length about 1·0 mm. ; genital segment a little longer than wide 9
Length 1·3–1·6 mm. ; genital segment about as long as wide 10
9 Caudal ramus 48 × 36 μ, ratio of 1·33 : 1 . . . . ***frequens***
Caudal ramus 60 × 28 μ, ratio of 2·14 : 1 . . . . ***astropectinis***
10 Caudal ramus 61 × 38 μ, ratio of 1·61 : 1 . . . . ***luidiae***
Caudal ramus 96 × 43 μ, ratio of 2·23 : 1 . . . . ***lautus***
11 Formula of endopod of fourth leg 0–0 ; II . . . . ***pollex***
Formula of endopod of fourth leg 0–1 ; II, I 12
12 With 2 posterior dorsal sclerotized elevations on genital segment . ***caeruleus***
Without such elevations 13
13 Free segment of leg 5 a little more than 3× longer than wide and slightly recurved ; length 1·41 mm. . . . . ***femineus***
Free segment of leg 5 less than 3× longer than wide and not recurved ; length 1·2 mm. or less 14
14 Ratio of length of prosome to urosome 1·87 : 1, ratio of length to width of prosome 1·45 : 1 . . . . ***kossmanni***
Ratio of length of prosome to urosome 2·4–3·3 : 1 ; ratio of length to width of prosome 0·94–1·22 : 1 15
15 Ratio of body length to width about 1·28 : 1 . . . . . . ***longicaudatus***
Ratio of body length to width about 1·5 : 1 16
16 Two setae on free segment of leg 5 about equal in length 17
Two setae on free segment of leg 5 distinctly unequal in length 18
17 Basis of leg 4 greatly elongated, ratio of its length to length of exopod about 13·5 : 5 ***pleurobranchi***
Basis of leg 4 not as elongated, ratio of its length to length of exopod about 9 : 5 ***oreastriphilus***
18 Postgenital segments and caudal rami together more than 4× as long as genital segment . . . . ***thorelli***
Postgenital segments and caudal rami together only a little longer than genital segment or shorter than that segment 19
19 Postgenital segments and caudal rami together a little longer than genital segment ***curticaudatus***
Postgenital segments and caudal rami together a little shorter than genital segment ***holothuriae***

Males

1 Three postgenital segments 2
Four postgenital segments 5
2 Caudal ramus distinctly elongated 3
Caudal ramus nearly quadrate 4

3 Caudal ramus 7·5 × longer than wide . . . . ***affinis***
Caudal ramus about 4 × longer than wide . . . . ***gracilis***
4 Caudal ramus slightly longer than wide ; claw of maxilliped evenly recurved ; free segment of leg 5 nearly 4 × longer than wide . species of Humes and Ho, in press
Caudal ramus a little wider than long ; claw of maxilliped with 2 slight flexures ; free segment of leg 5 about 2 × longer than wide . . . . . ***longiseta***
5 With more than 1 claw on last segment of second antenna 6
With only 1 claw on last segment of second antenna 10
6 With 3 claws on last segment of second antenna 7
With 2 claws on last segment of second antenna . . . . . . ***clausi***
7 Length less than 1 mm. ; free segment of leg 5 about 24–25 × 12 μ 8
Length somewhat more than 1 mm. ; free segment of leg 5 about 36–38 × 17 μ . 9
8 Caudal ramus a little longer than wide, ratio about 1·3 : 1 . . ***frequens***
Caudal ramus more elongated, ratio about 2·1 : 1 . . . . . ***astropectinis***
9 Caudal ramus somewhat elongated, ratio about 1·6 : 1 . . . . ***luidiae***
Caudal ramus more elongated, ratio about 2·2 : 1 . . . . . . ***lautus***
10 With thumb-like process on third segment of second antenna ; formula of endopod of fourth leg 0–0 ; II . . . . ***pollex***
Without thumb-like process on third segment of second antenna ; formula of endopod of fourth leg 0–1 ; II, 1 11
11 Maxilliped not elongated, 2- or 3-segmented, with relatively short claw . . 12
Maxilliped elongated, 4-segmented, with long prehensile claw 14
12 Maxilliped small, 2-segmented, with relatively small but distinctly prehensile claw 13
Maxilliped female-like, 3-segmented, with terminal spiniform process instead of a claw ***femineus***
13 First segment of second maxilla with 3 peculiar sclerotized processes . ***caeruleus***
First segment of second maxilla without such processes . . . ***holothuriae***
14 Segment of leg 5 and genital segment separated . . . . . . ***kossmanni***
Segment of leg 5 and genital segment almost completely fused . ***oreastriphilus***

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EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

Abbreviations used : A_1 = first antenna, A_2 = second antenna, MD = mandible, P = paragnath, MX_1 = first maxilla, MX_2 = second maxilla, MXPD = maxilliped, P_1 = leg 1.

PLATE 1

Stellicola kossmanni n. sp., female

FIG. 1. Dorsal (A).
FIG. 2. Marginal membrane on prosomal segments, dorsal (B).
FIG. 3. Urosome, dorsal (C).
FIG. 4. Area of attachment of egg sac, dorsal (D).
FIG. 5. Caudal ramus and part of anal segment, dorsal (E).
FIG. 6. Rostral area, ventral (C).

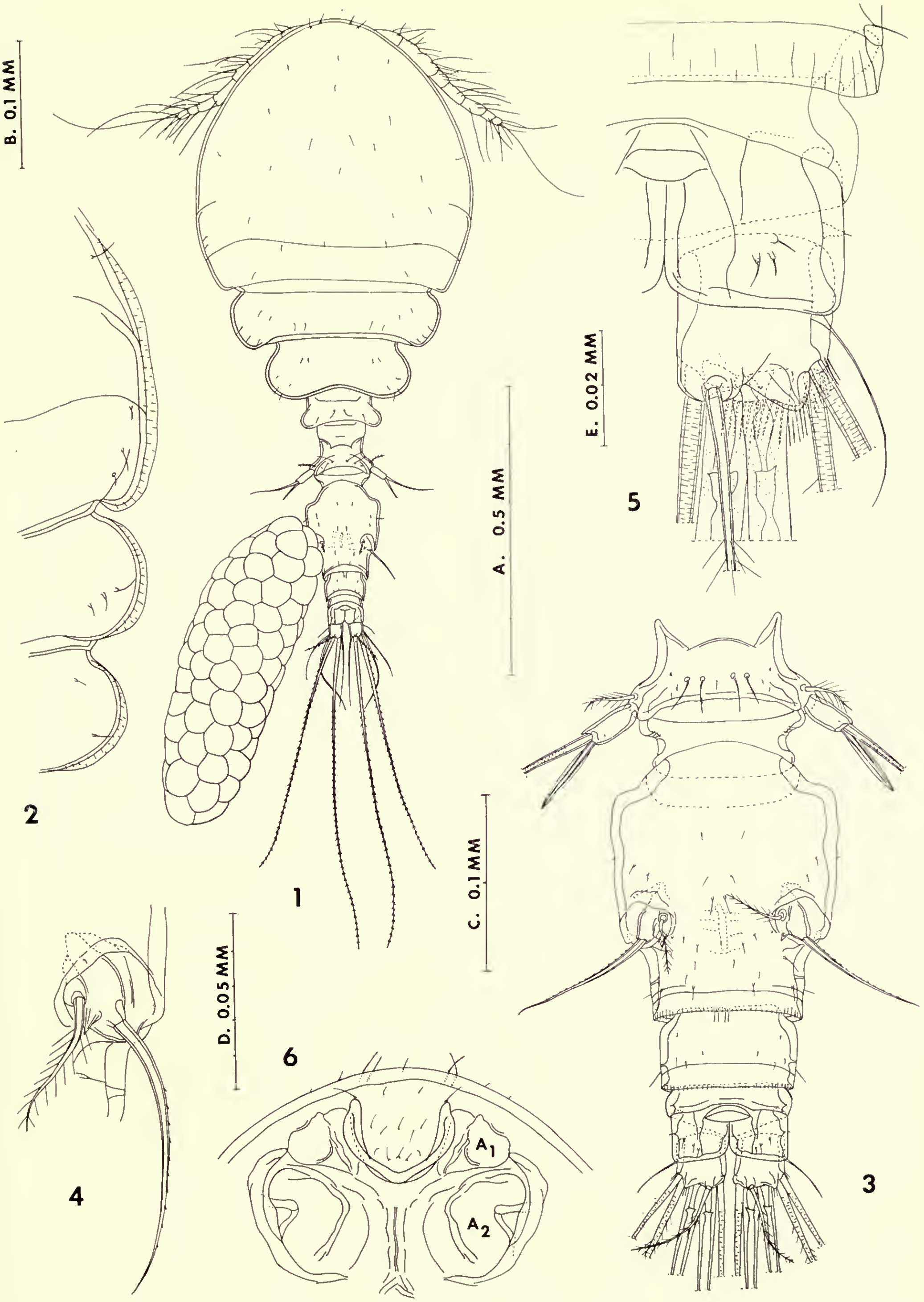

B. 0.1 MM
E. 0.02 MM
5
A. 0.5 MM
2
1
C. 0.1 MM
D. 0.05 MM
6
A1
A2
4
3

PLATE 2

Stellicola kossmanni n. sp., female (continued)

Fig. 7. First antenna, anterodorsal (C).
Fig. 8. Second antenna, anterior (F).
Fig. 9. Labrum, ventral (D).
Fig. 10. Mandible, posterior (D).
Fig. 11. First maxilla, posterolateral (G).
Fig. 12. Second maxilla, posterior (D).
Fig. 13. Maxilliped, anterior (D).
Fig. 14. Area between maxillipeds and first pair of legs, ventral (C).
Fig. 15. Leg 1 and intercoxal plate, anterior (C).

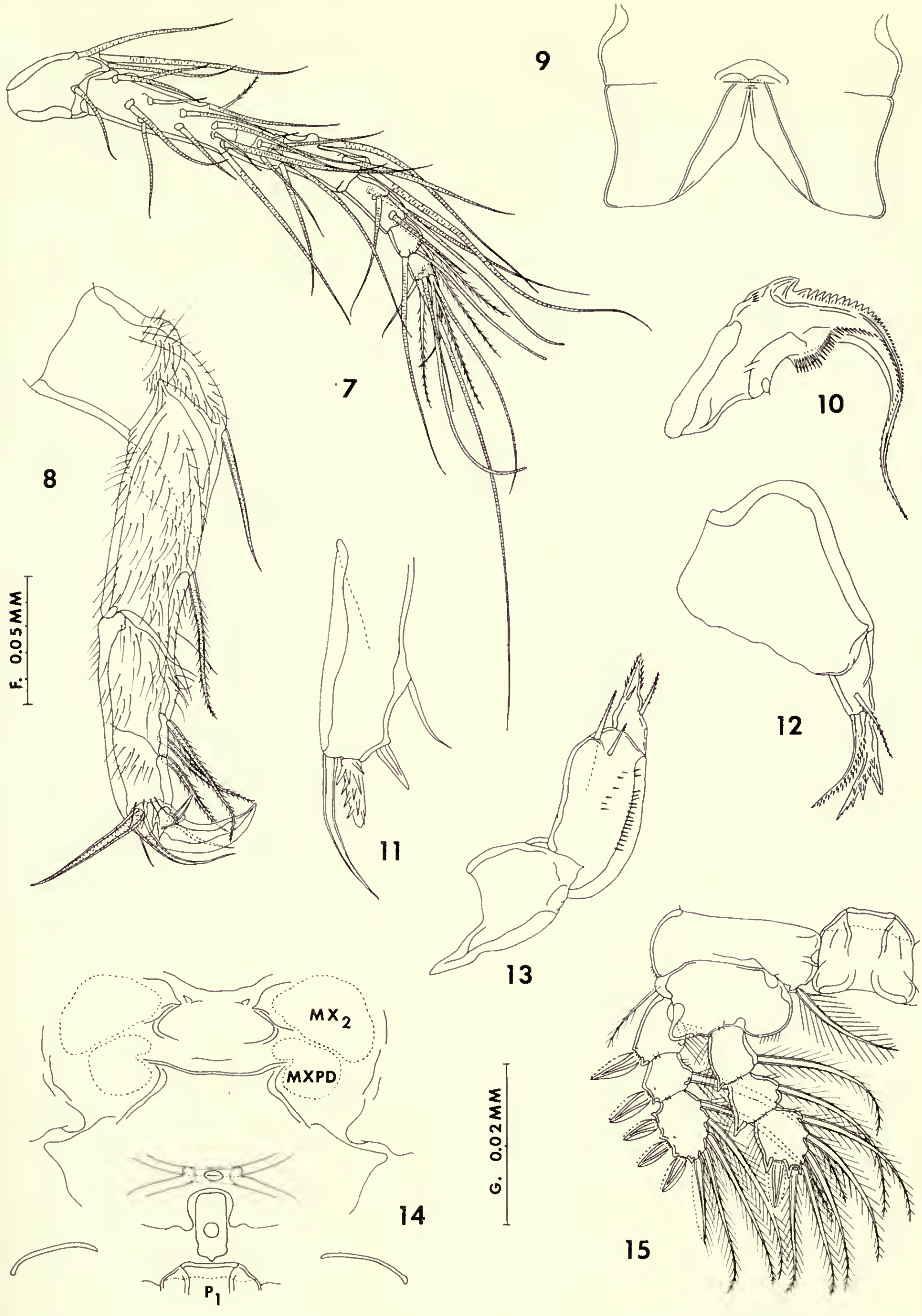

F. 0.05 MM
G. 0.02 MM
MX_2
MXPD
P_1

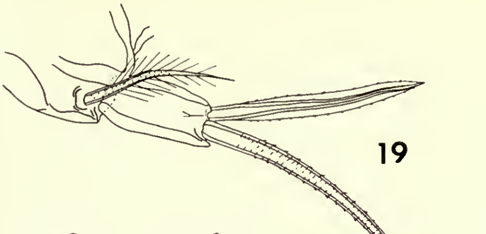
PLATE 3

Stellicola kossmanni n. sp., female (continued)

FIG. 16. Leg 2, anterior (C).
FIG. 17. Leg 3, anterior (C).
FIG. 18. Leg 4 and intercoxal plate, anterior (C).
FIG. 19. Leg 5, dorsal (D).

Stellicola kossmanni n. sp., male

FIG. 20. Dorsal (A).
FIG. 21. Urosome, dorsal (C).



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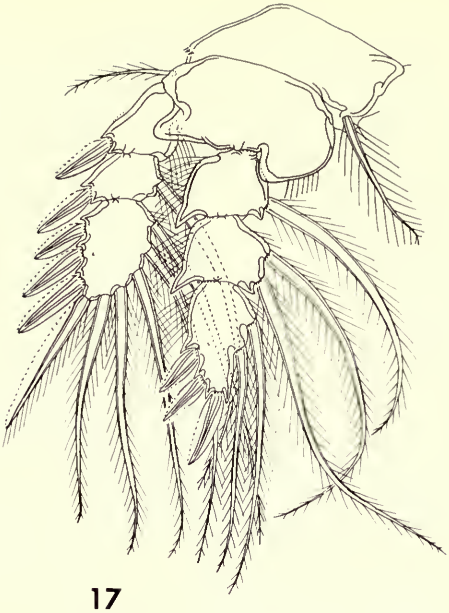

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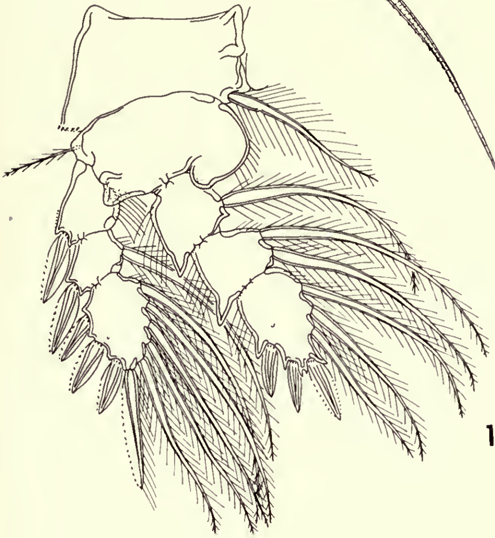

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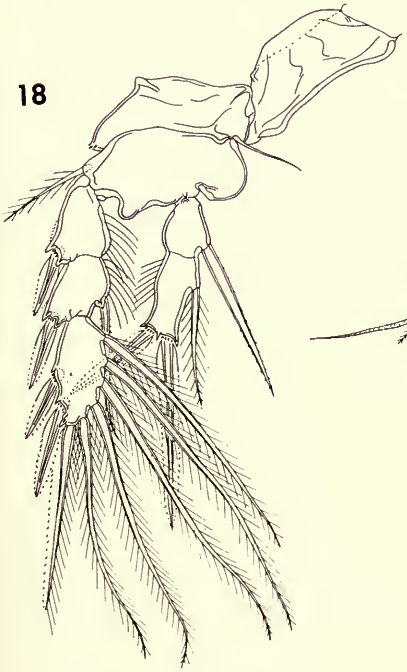

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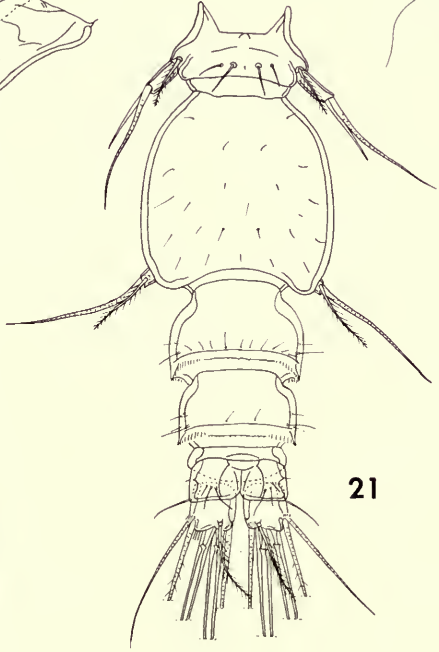

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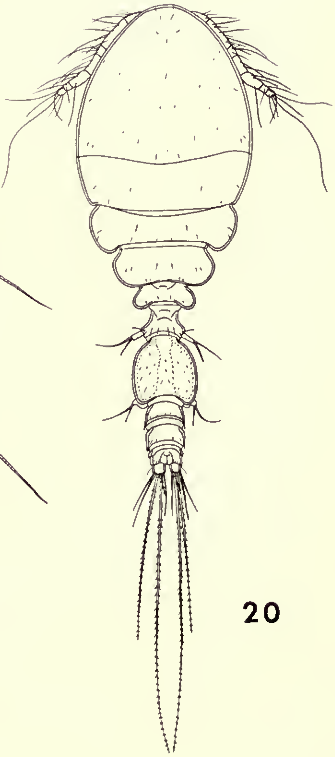

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PLATE 4

Stellicola kossmanni n. sp., male (continued)

FIG. 22. Maxilliped, anterior (F).
FIG. 23. Leg 6, ventral (F).
FIG. 24. Spermatophore, in body of male, dorsal (C).

Stellicola affinis n. sp., female

FIG. 25. Dorsal (A).
FIG. 26. Lateral (A).
FIG. 27. Urosome, dorsal (B).
FIG. 28. Area of attachment of egg sac, dorsal (D).
FIG. 29. Caudal ramus, dorsal (F).
FIG. 30. Rostrum, ventral (C).
FIG. 31. First antenna, anterodorsal (C).

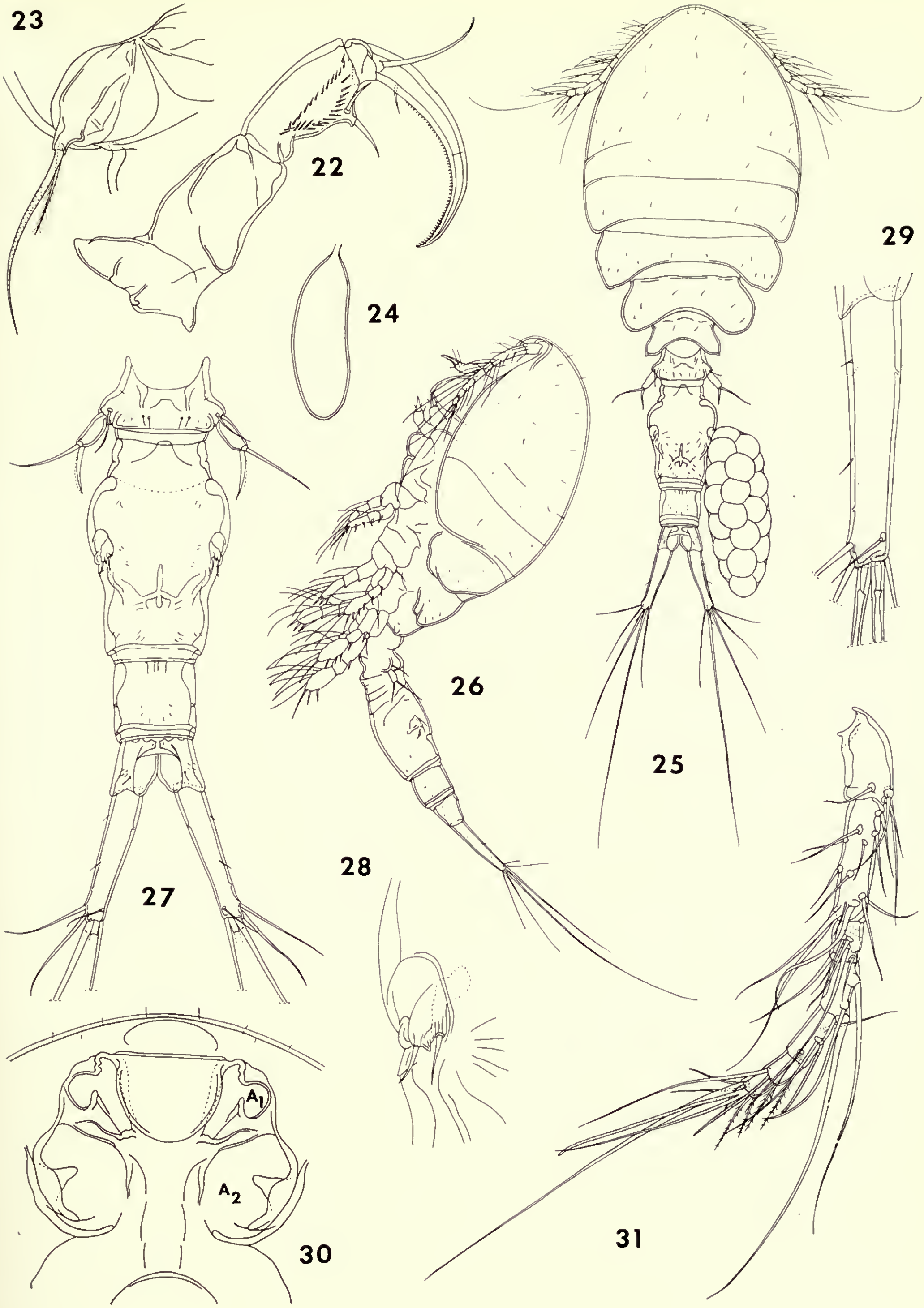
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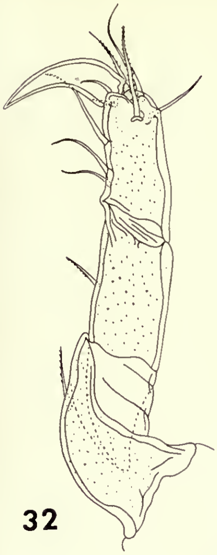
PLATE 5

Stellicola affinis n. sp., female (continued)

Fig. 32. Second antenna, posterior (F).
Fig. 33. Labrum, ventral (D).
Fig. 34. Mandible, posterior (D).
Fig. 35. First maxilla, posterior (E).
Fig. 36. Second maxilla, posterior (D).
Fig. 37. Maxilliped, posterior (D).
Fig. 38. Oral and postoral areas, ventral (C).
Fig. 39. Leg 1 and intercoxal plate, anterior (C).
Fig. 40. Leg 2, anterior (C).
Fig. 41. Leg 3, anterior (C).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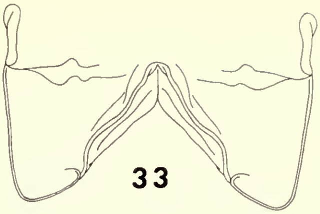
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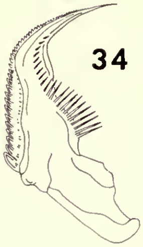
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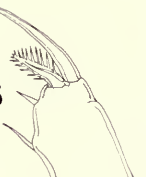
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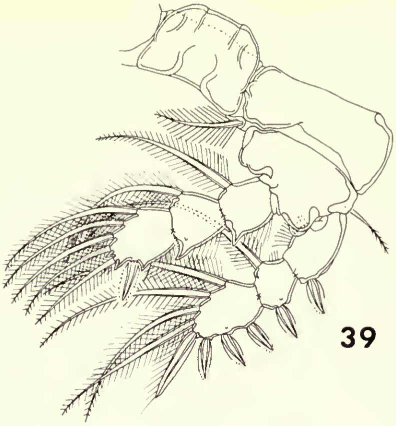
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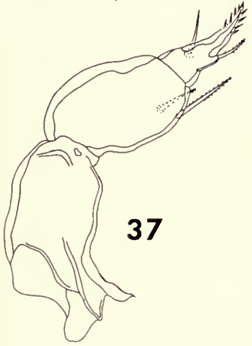
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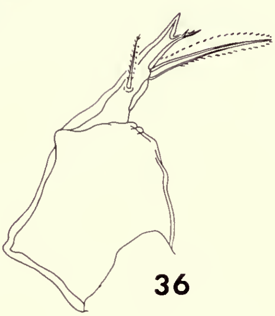
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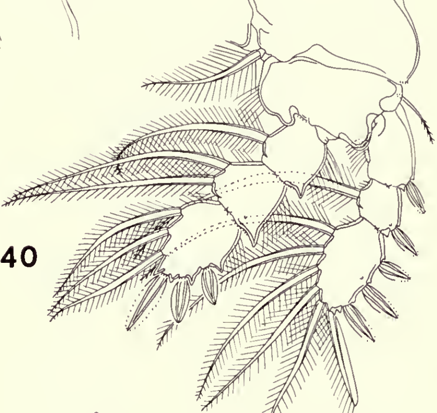
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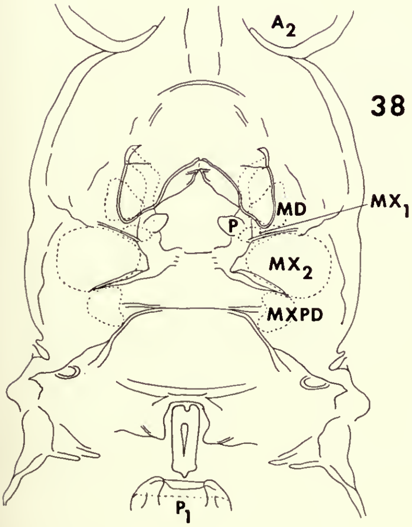
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A_2
MD
MX_1
P
MX_2
MXPD
P_1

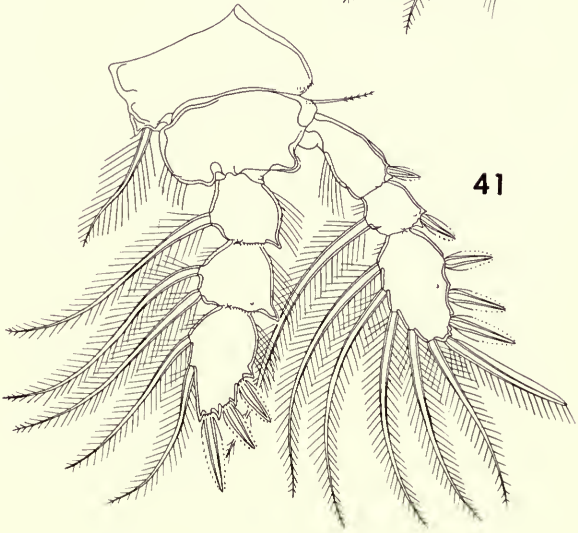
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PLATE 6

Stellicola affinis n. sp., female (continued)

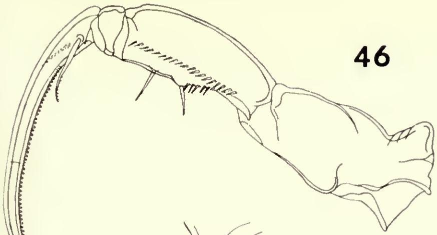
FIG. 42. Leg 4 and intercoxal plate, anterior (C).
FIG. 43. Leg 5, dorsal (D).

Stellicola affinis n. sp., male

FIG. 44. Dorsal (A).
FIG. 45. Urosome, dorsal (B).
FIG. 46. Maxilliped, anterior (F).
FIG. 47. Leg 5, ventral (D).
FIG. 48. Leg 6, ventral (F).

Stellicola longiseta n. sp., female

FIG. 49. Dorsal (H).
FIG. 50. Urosome, dorsal (B).



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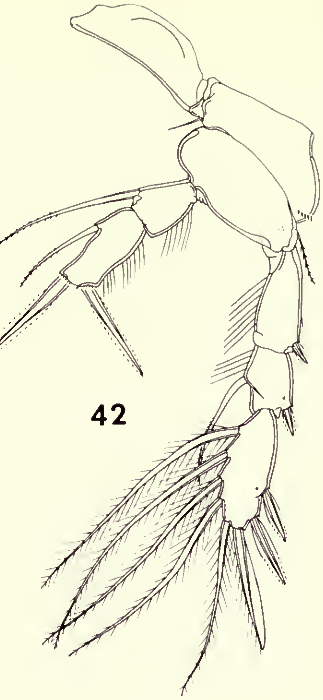

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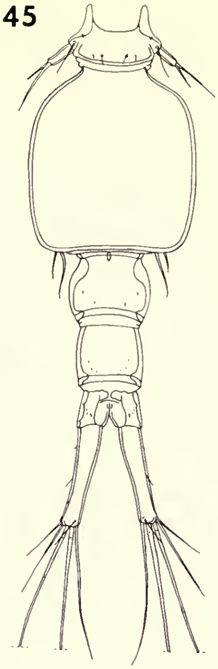

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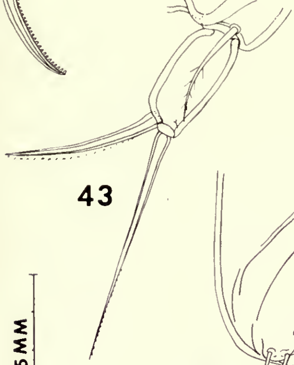

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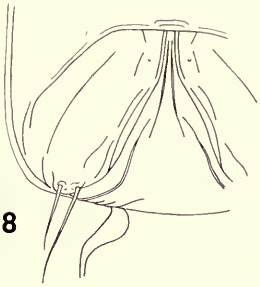

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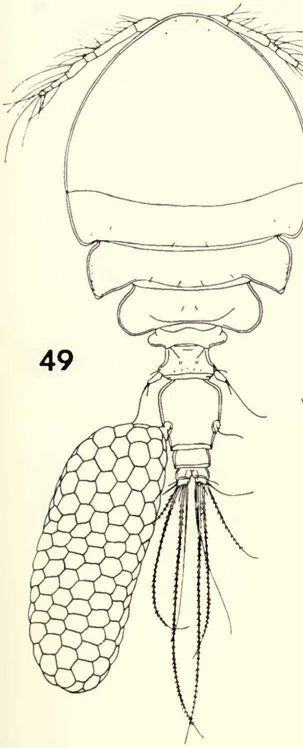
H. 0.5 MM



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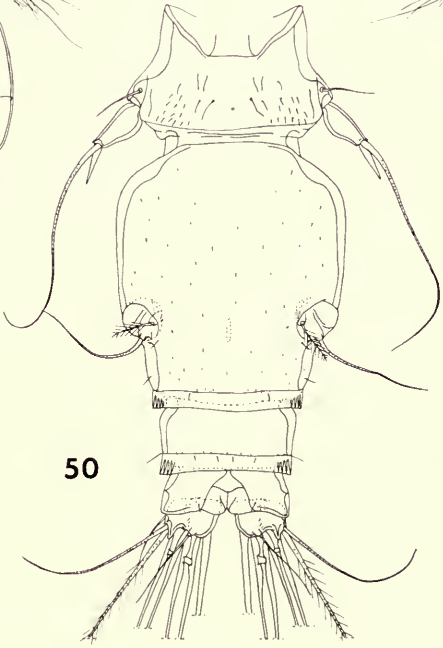

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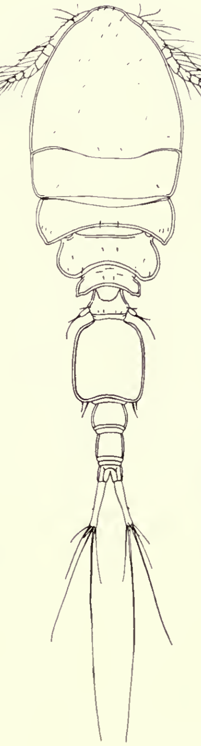

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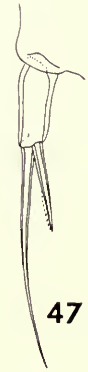

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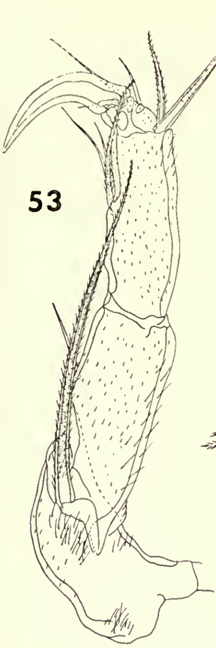
PLATE 7

Stellicola longiseta n. sp., female (continued)

FIG. 51. Caudal ramus, dorsal (E).
FIG. 52. Rostrum, ventral (C).
FIG. 53. Second antenna, anterior (F).
FIG. 54. Labrum, ventral (F).
FIG. 55. Mandible, posterior (D).
FIG. 56. Second maxilla, posterior (D).
FIG. 57. Maxilliped, anterior (D).
FIG. 58. Last segment of endopod of leg 2, anterior (F).
FIG. 59. Last segment of endopod of leg 3, anterior (F).
FIG. 60. Leg 4 and intercoxal plate, anterior (C).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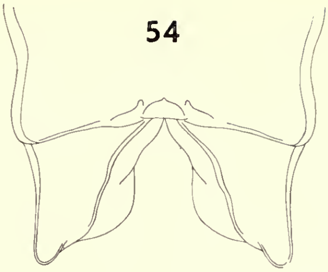
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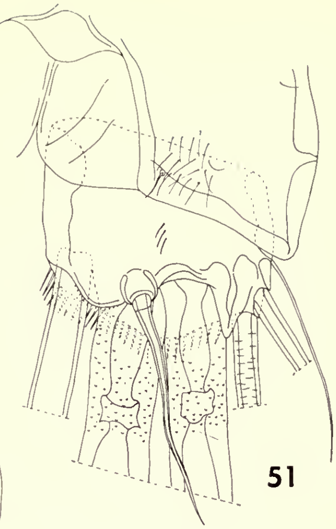
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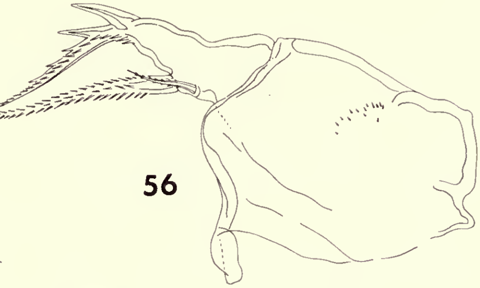
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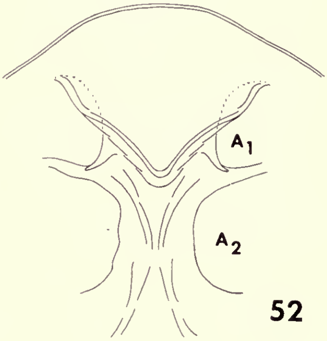

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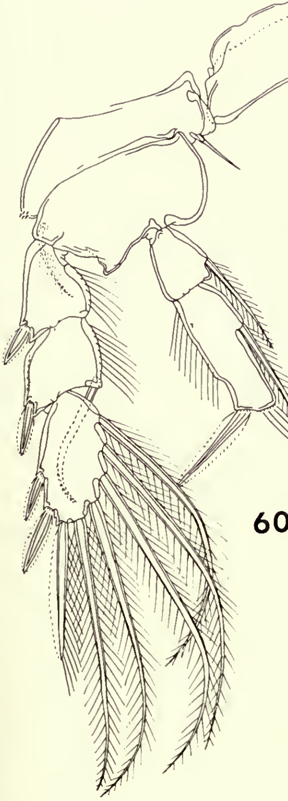
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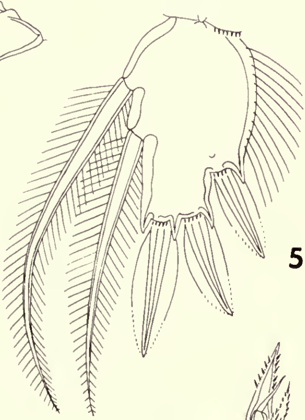
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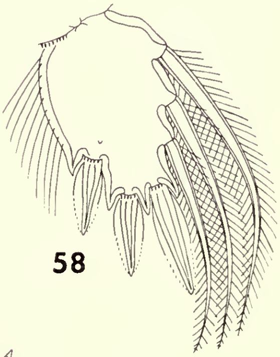
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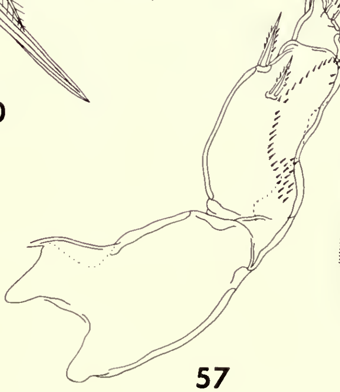
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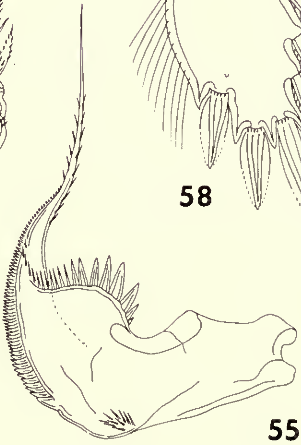
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PLATE 8

Stellicola longiseta n. sp., female (continued)

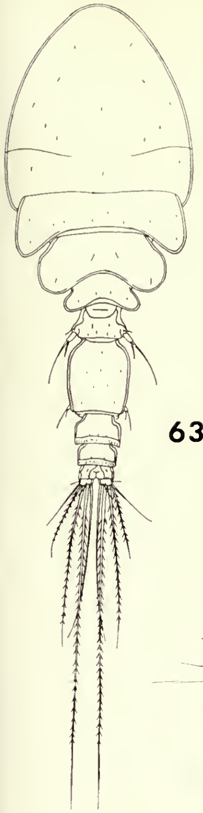
Fig. 61. Endopod of leg 4, anterior (F).
Fig. 62. Leg 5, dorsal (D).

Stellicola longiseta n. sp., male

Fig. 63. Dorsal (A).
Fig. 64. Urosome, dorsal (C).
Fig. 65. Maxilliped, anterior (F).
Fig. 66. Leg 5, dorsal (E).

Stellicola femineus n. sp., female

Fig. 67. Dorsal (H).



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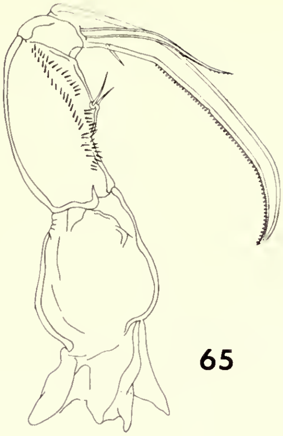

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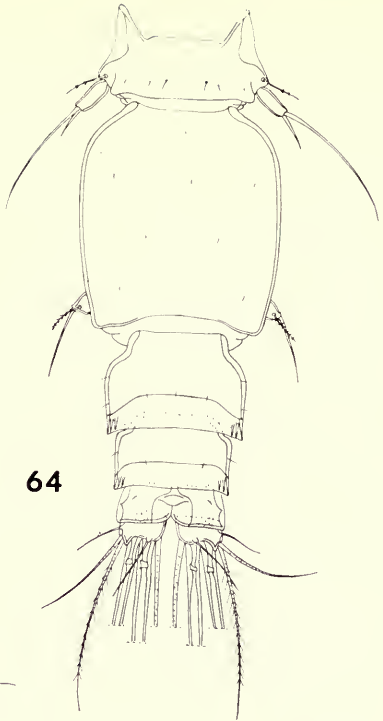

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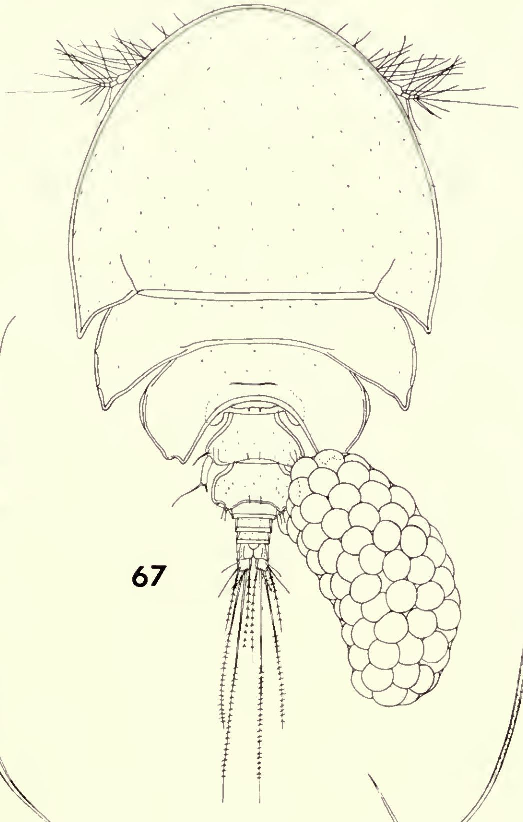

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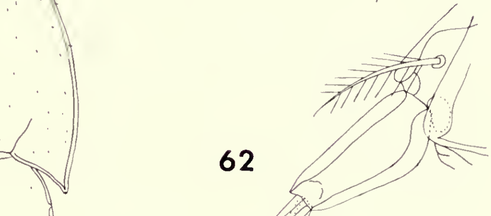

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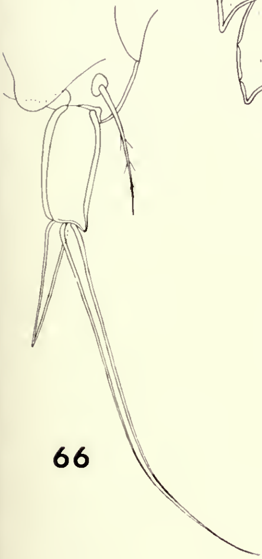

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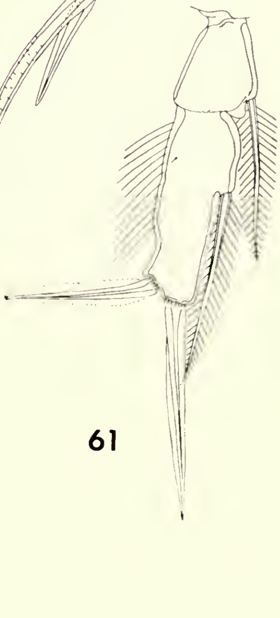

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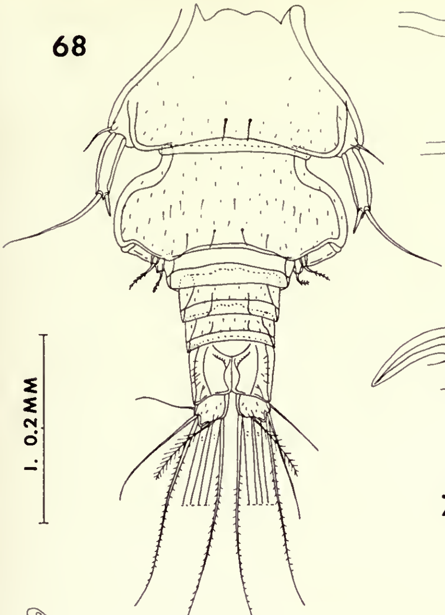
PLATE 9

Stellicola femineus n. sp., female (continued)

FIG. 68. Urosome, dorsal (I).
FIG. 69. Area of attachment of egg sac, dorsal (F).
FIG. 70. Caudal ramus, dorsal (E).
FIG. 71. Rostrum, oral and postoral areas, mouthparts not labelled but in same relative positions as in Plate 5, fig. 38, ventral (A).
FIG. 72. First antenna, dorsal (C).
FIG. 73. Second antenna, posterior (B).
FIG. 74. Tip of second antenna, anterior (F).
FIG. 75. Labrum, ventral (C).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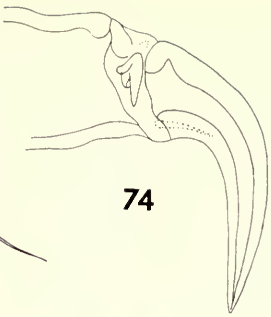
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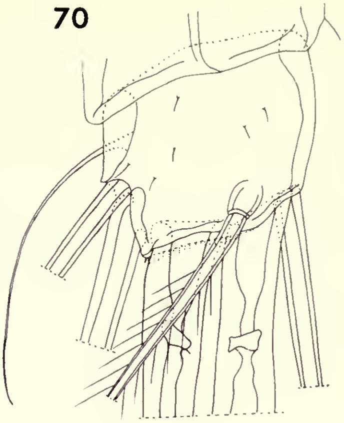
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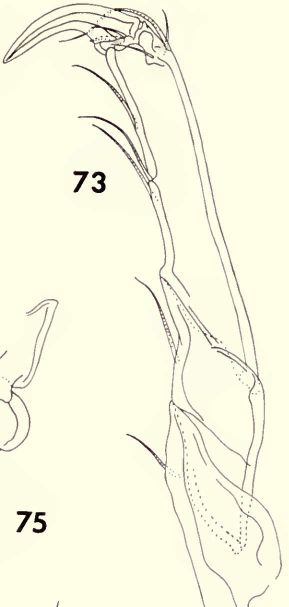
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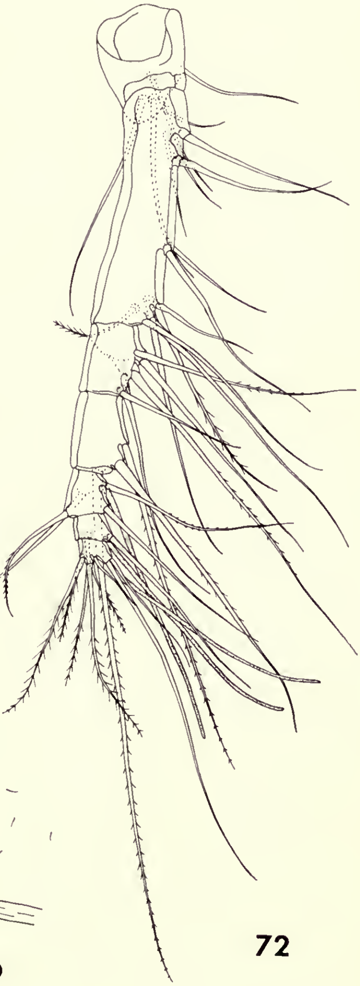
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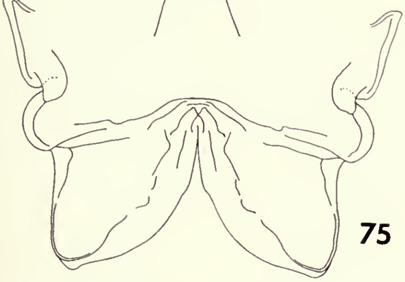
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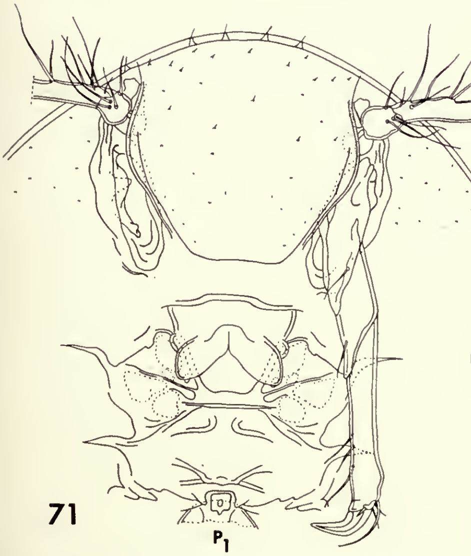
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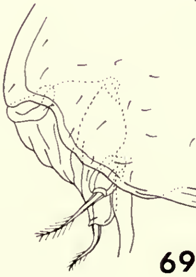
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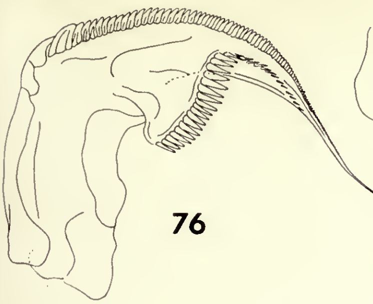
PLATE 10

Stellicola femineus n. sp., female (continued)

Fig. 76. Mandible, posterior (F).
Fig. 77. First maxilla, anterolateral (F).
Fig. 78. Second maxilla, posterior (F).
Fig. 79. Maxilliped, posterior (F).
Fig. 80. Leg 1 and intercoxal plate, anterior (B).
Fig. 81. Leg 2, anterior (B).
Fig. 82. Leg 3, anterior (B).
Fig. 83. Leg 4 and intercoxal plate, anterior (B).
Fig. 84. Endopod of leg 4, anterior (F).



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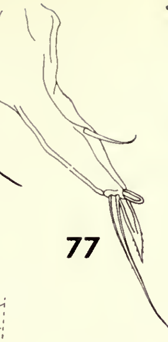

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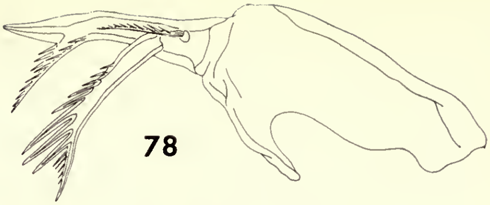

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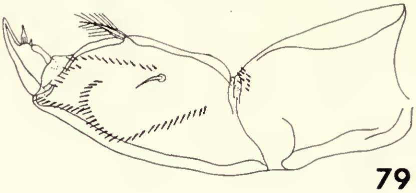

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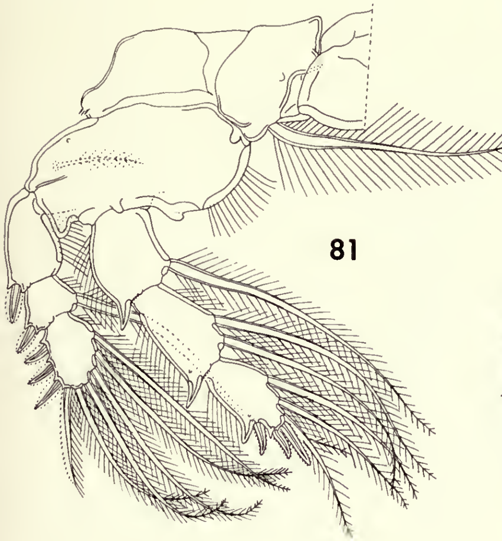

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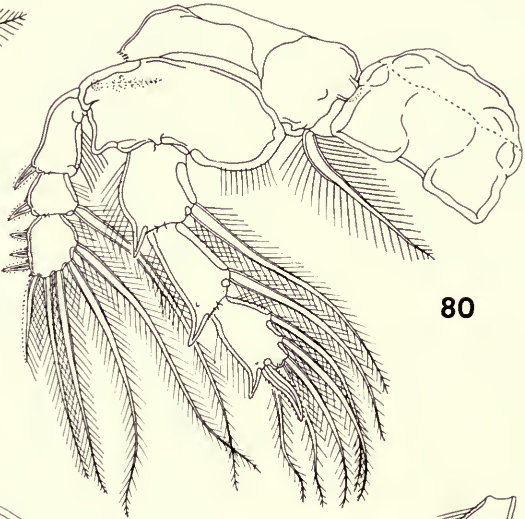

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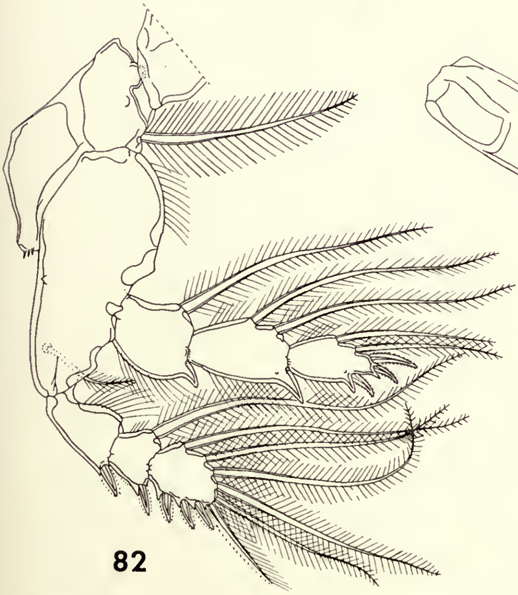

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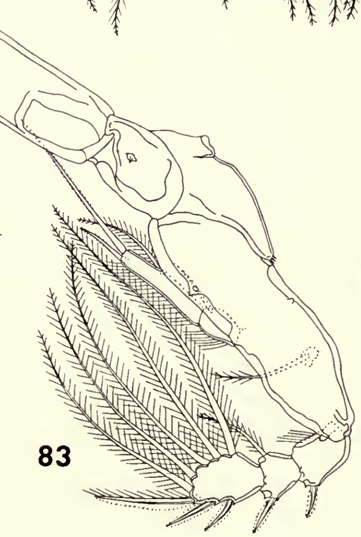

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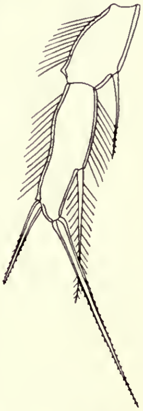

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PLATE 11

Stellicola femineus n. sp., female (continued)

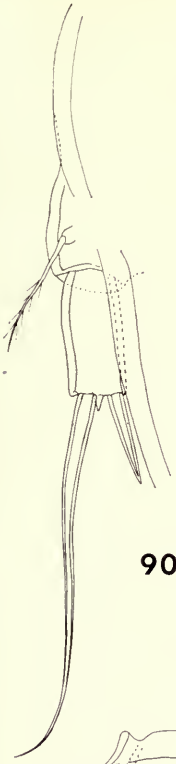
Fig. 85. Leg 5, dorsal (F).

Stellicola femineus n. sp., male

Fig. 86. Dorsal (A).
Fig. 87. Urosome, dorsal (B).
Fig. 88. Labrum, ventral (F).
Fig. 89. Maxilliped, postero-inner (D).
Fig. 90. Leg 5, dorsal (E).
Fig. 91. Leg 6, ventral (F).
Fig. 92. Spermatophore, inside male, dorsal (B).

Stellicola pollex n. sp., female

Fig. 93. Dorsal (H).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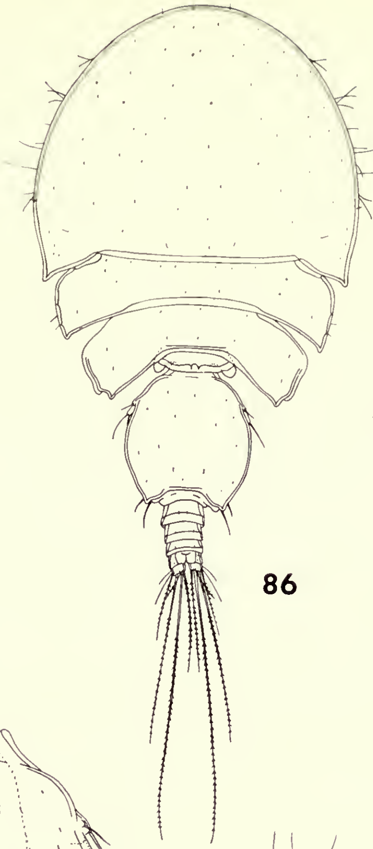
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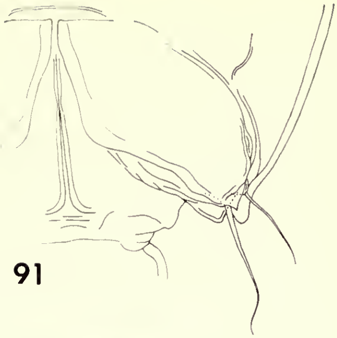
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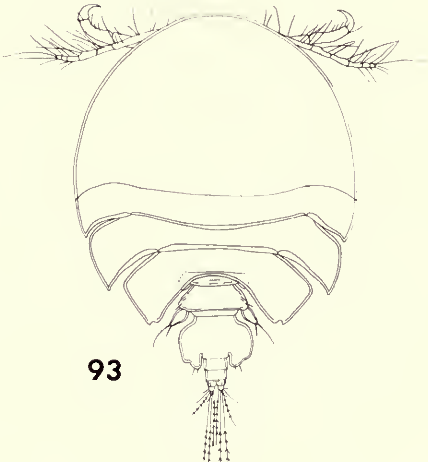
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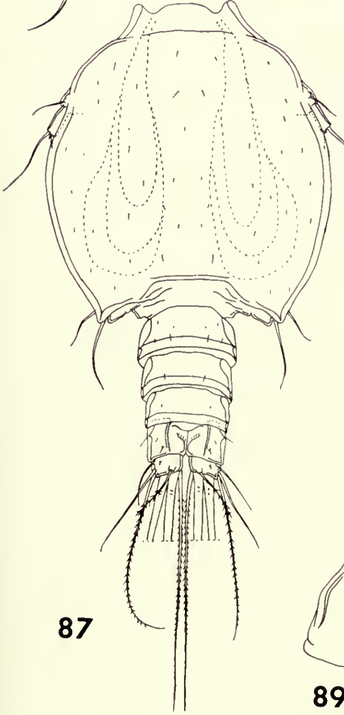
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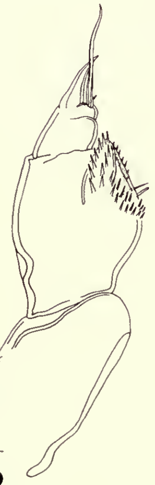
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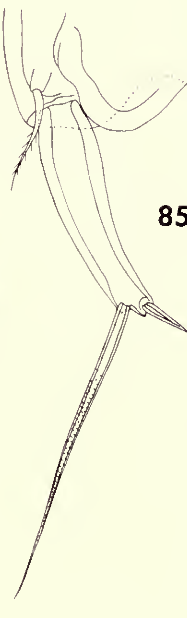
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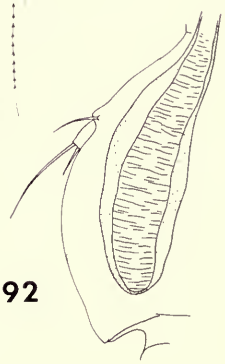
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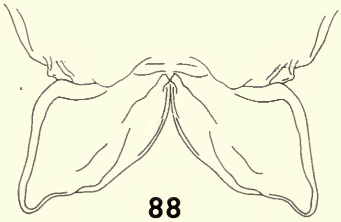
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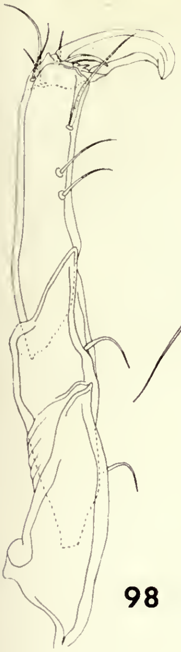
PLATE 12

Stellicola pollex n. sp., female (continued)

FIG. 94. Urosome, dorsal (C).
FIG. 95. Area of attachment of egg sac, ventral (D).
FIG. 96. Caudal ramus, dorsal (E).
FIG. 97. First antenna, ventral (C).
FIG. 98. Second antenna, posterior (C).
FIG. 99. Mandible, posterior (F).
FIG. 100. Paragnath, ventral (G).
FIG. 101. Second maxilla, posterior (D).



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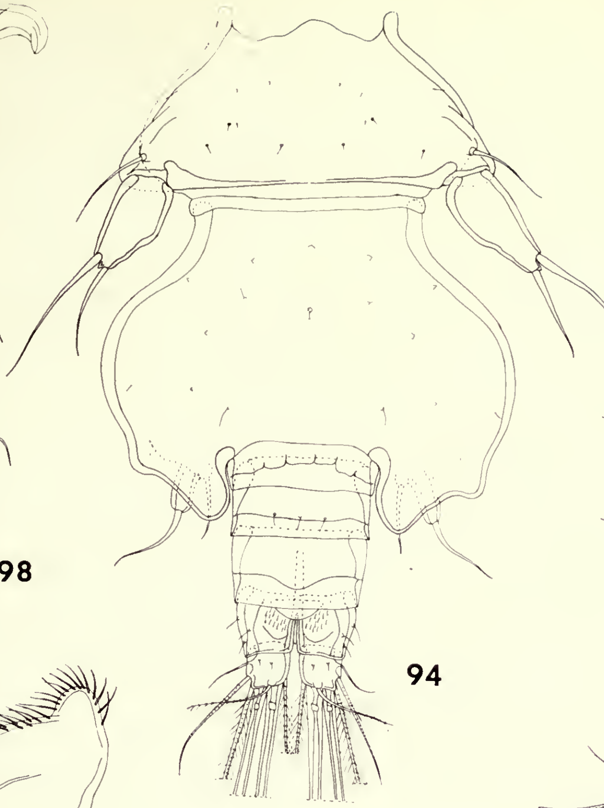

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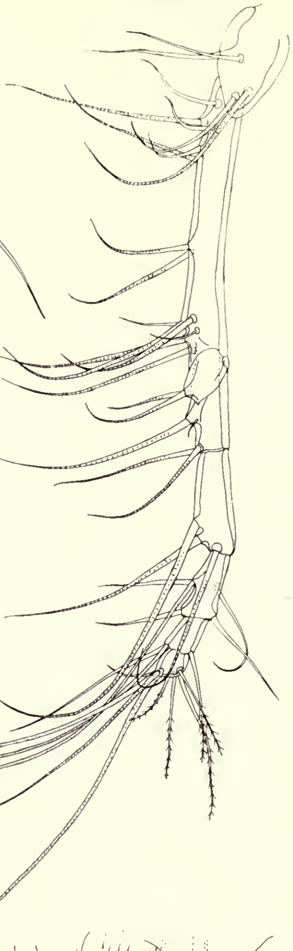

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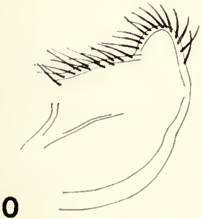

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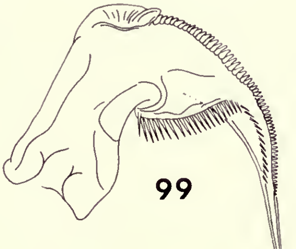

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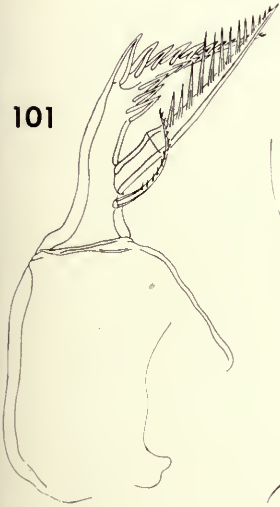

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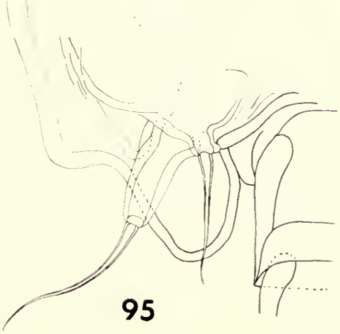

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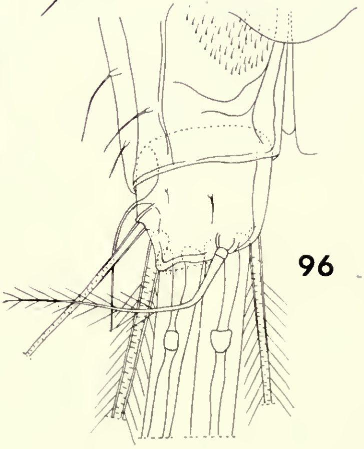

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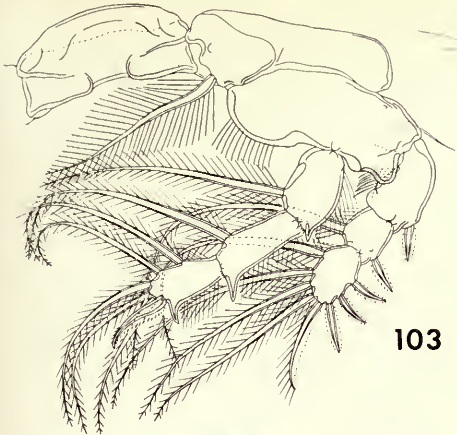
PLATE 13

Stellicola pollex n. sp., female (continued)

FIG. 102. Maxilliped, posterior (D).
FIG. 103. Leg 1 and intercoxal plate, anterior (C).
FIG. 104. Leg 2, anterior (C).
FIG. 105. Leg 3, anterior (C).
FIG. 106. Leg 4 and intercoxal plate, anterior (C).
FIG. 107. Endopod of leg 4, anterior (E).
FIG. 108. Leg 5, dorsal (D).

Stellicola pollex n. sp., male

FIG. 109. Dorsal (I).



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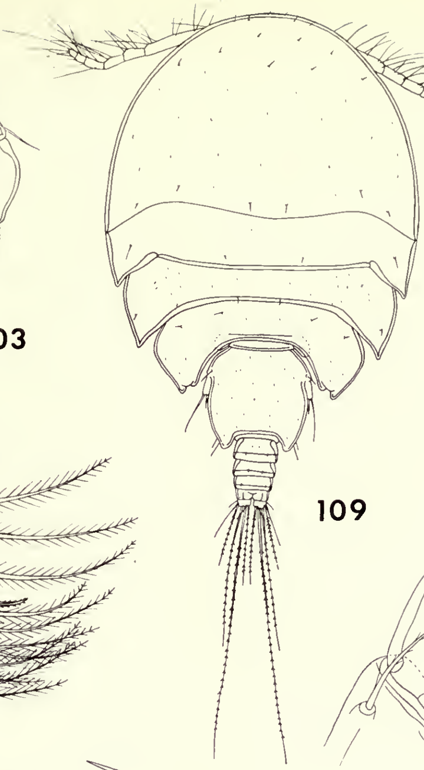

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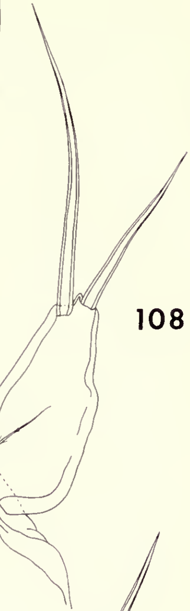

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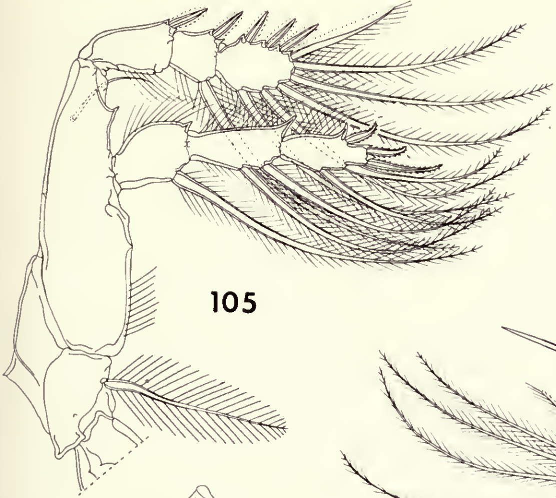

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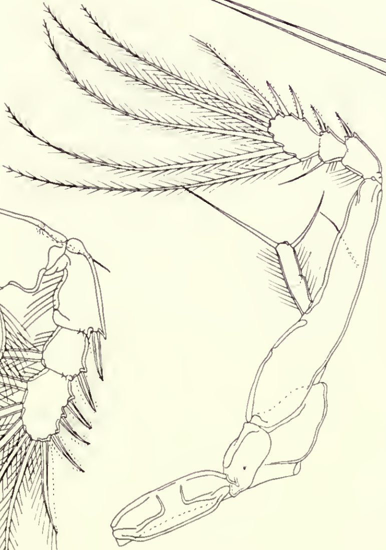

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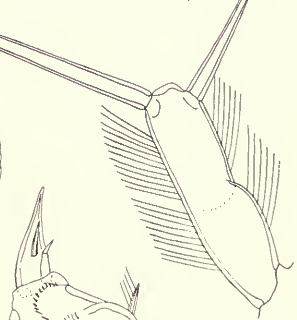

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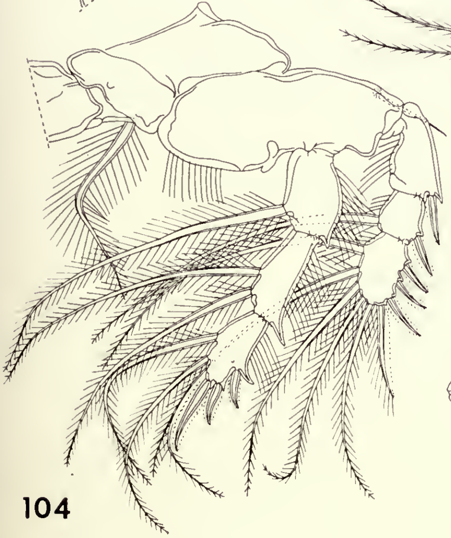

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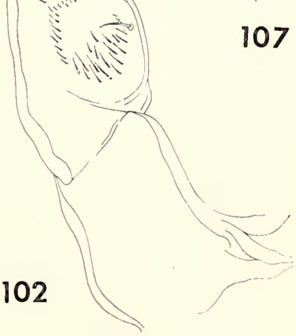

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PLATE 14

Stellicola pollex n. sp., male (continued)

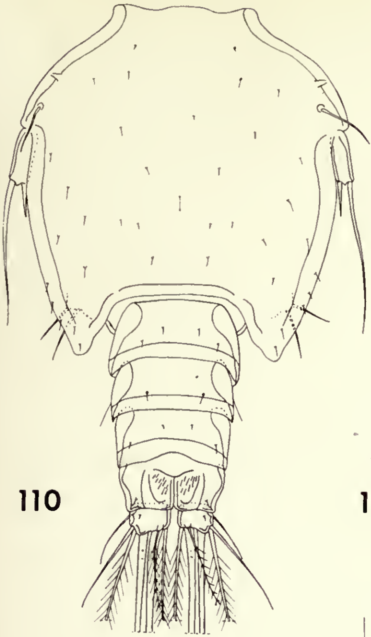
FIG. 110. Urosome, dorsal (F).
FIG. 111. Third segment of second antenna, anterior (E).
FIG. 112. Maxilliped, postero-inner (D).
FIG. 113. Leg 5, dorsal (G).
FIG. 114. Leg 6, ventral (D).

Stellicola oreastriphilus Kossmann, 1877, female

FIG. 115. Genital segment, dorsal (C).
FIG. 116. Tip of second antenna, posterior (F).
FIG. 117. Paragnath, ventral (E).
FIG. 118. Maxilliped, anterior (D).
FIG. 119. Endopod of leg 4, anterior (F).

Stellicola oreastriphilus Kossmann, 1877, male

FIG. 120. Segment of leg 5 and genital segment, dorsal (C).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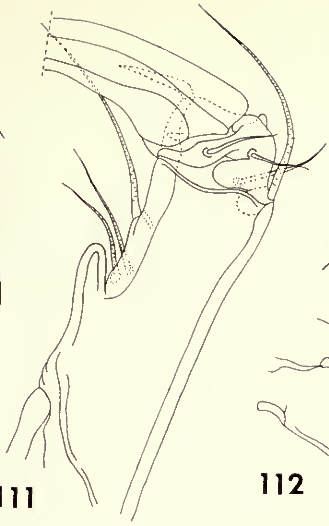
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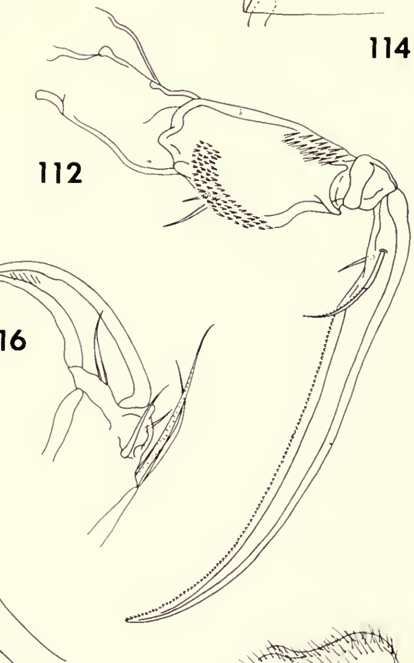
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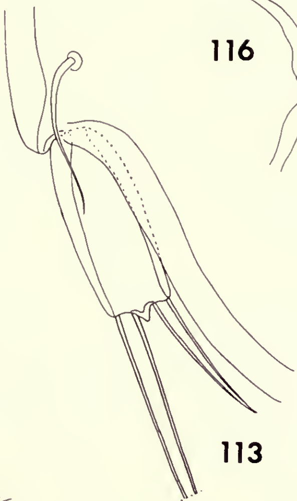
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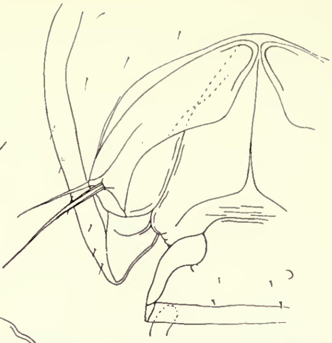
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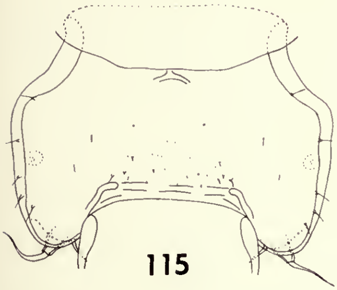
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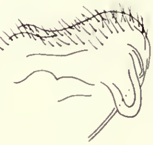
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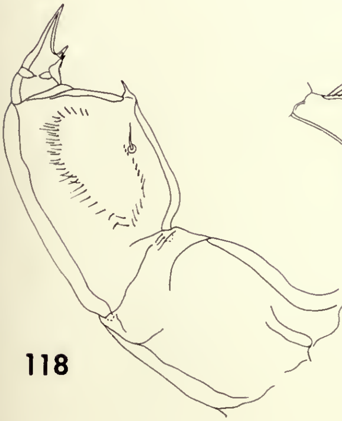
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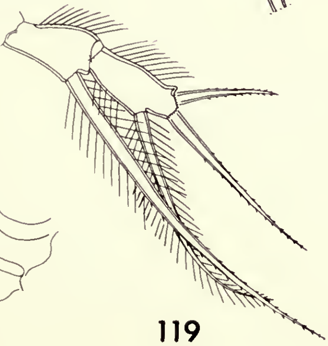
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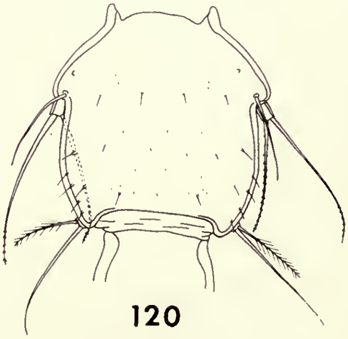
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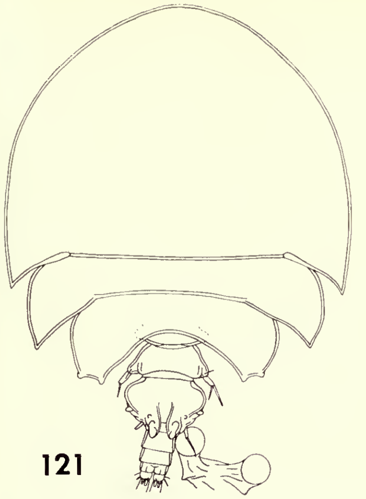
PLATE 15

Stellicola caeruleus (Stebbing, 1900), syntypic female

FIG. 121. Dorsal (H).
FIG. 122. Urosome, dorsal (B).
FIG. 123. Caudal ramus, dorsal (E).
FIG. 124. Rostrum and labrum, ventral (I).
FIG. 125. First antenna, ventral (C).
FIG. 126. Second antenna, anterior (B).
FIG. 127. Mandible, posterior (F).
FIG. 128. Second maxilla, posterior (F).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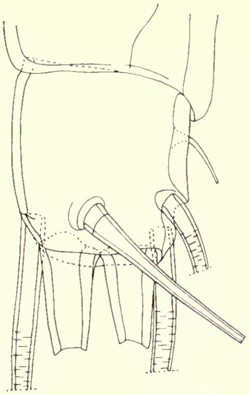
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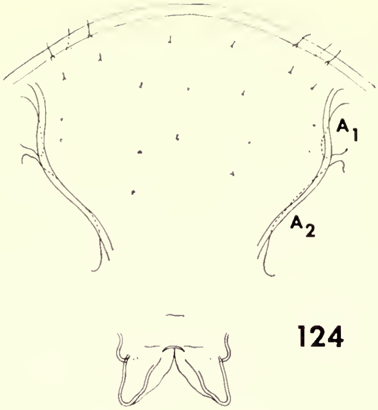

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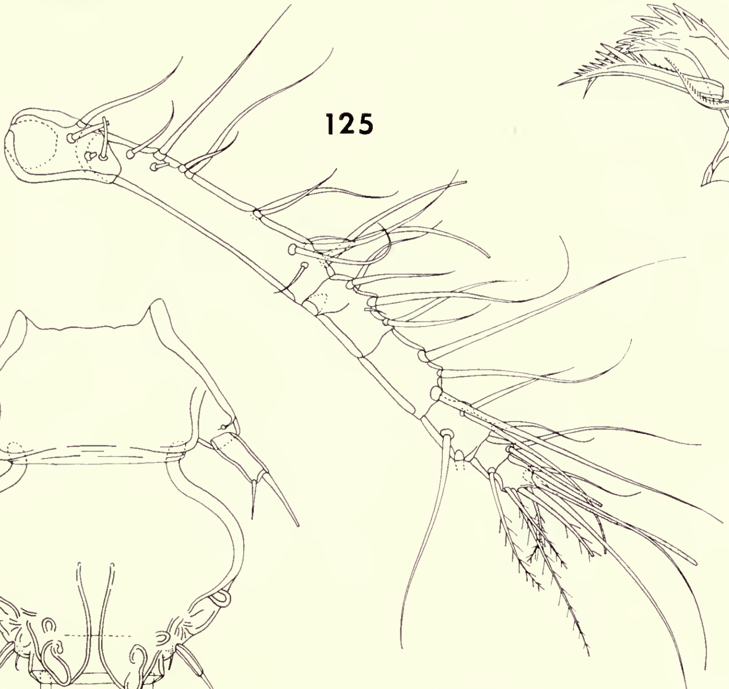
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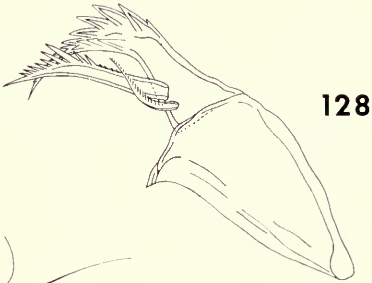
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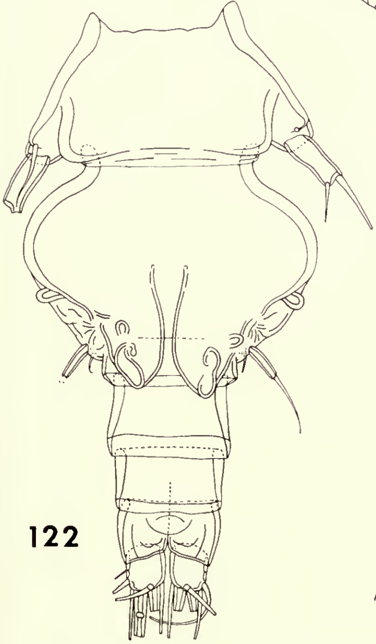
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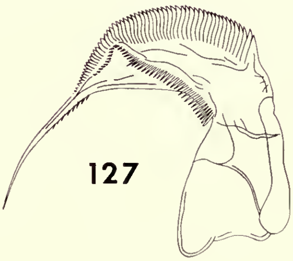
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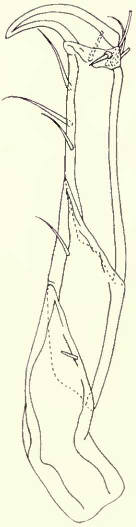
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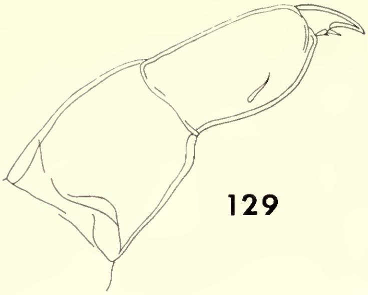
PLATE 16

Stellicola caeruleus (Stebbing, 1900), syntypic female (continued)

Fig. 129. Maxilliped, posterior (F).
Fig. 130. Leg 1 and intercoxal plate, anterior (C).
Fig. 131. Leg 2, anterior (C).
Fig. 132. Leg 3, anterior (C).
Fig. 133. Leg 4, anterior (F).
Fig. 134. Leg 5, dorsal (D).



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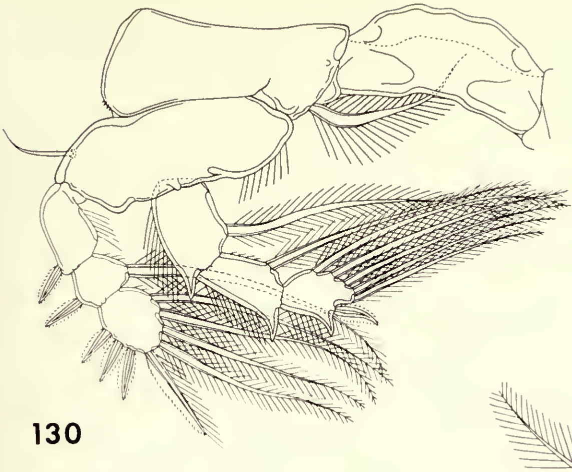

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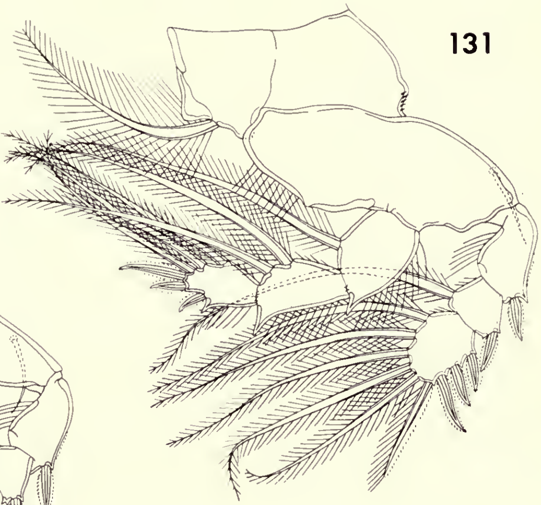

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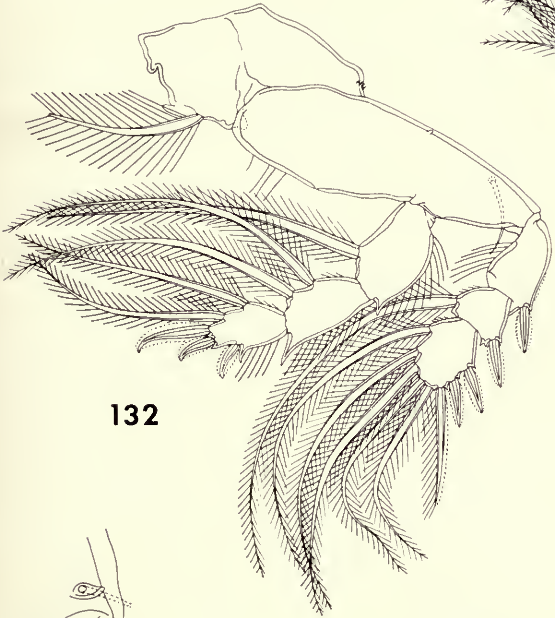

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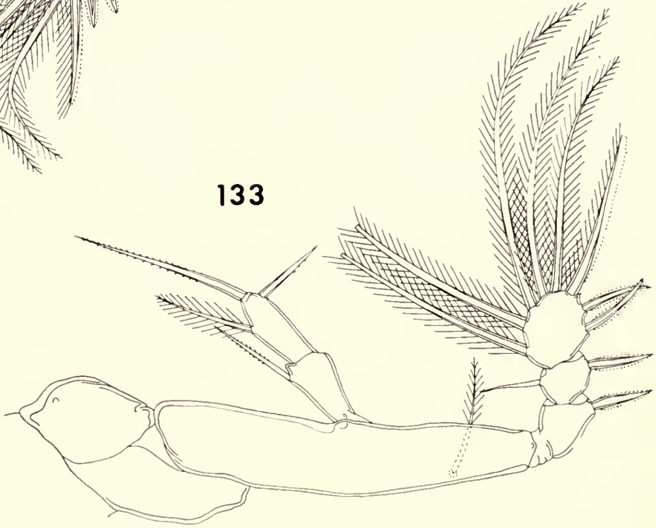

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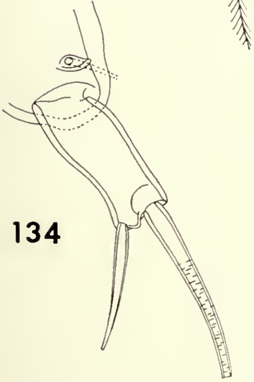

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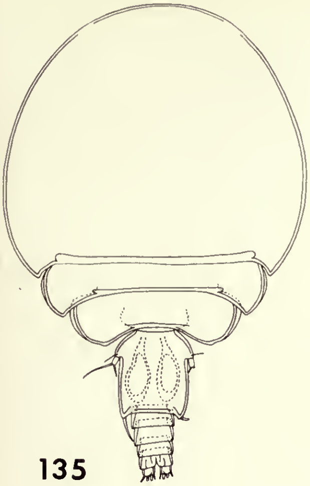
PLATE 17

Stellicola caeruleus (Stebbing, 1900) syntypic male

FIG. 135. Dorsal (I).
FIG. 136. Urosome, dorsal (F).
FIG. 137. Rostrum, ventral (C).
FIG. 138. Second maxilla, dorsal (E).
FIG. 139. Maxilliped, dorsal (G).
FIG. 140. Leg 5, dorsal (G).
FIG. 141. Leg 6, ventral (E).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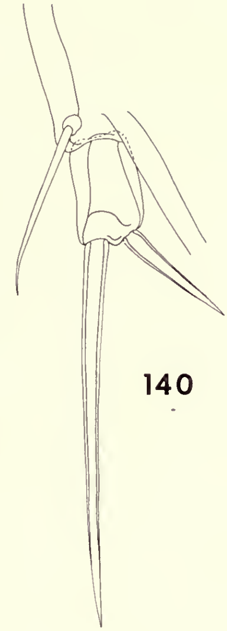
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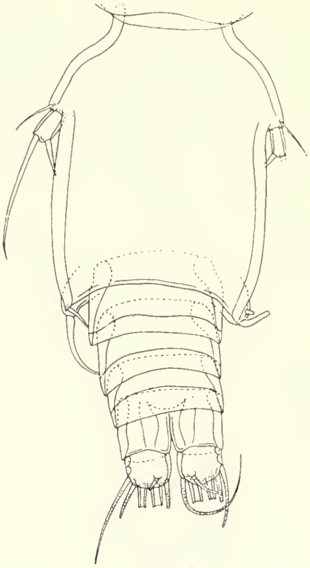
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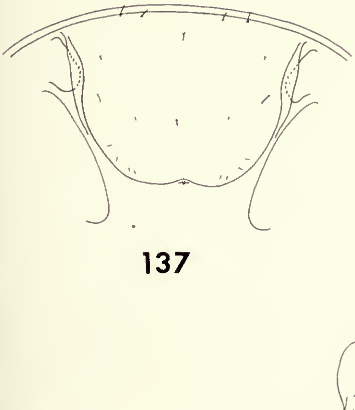
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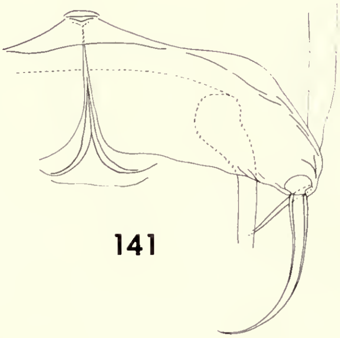
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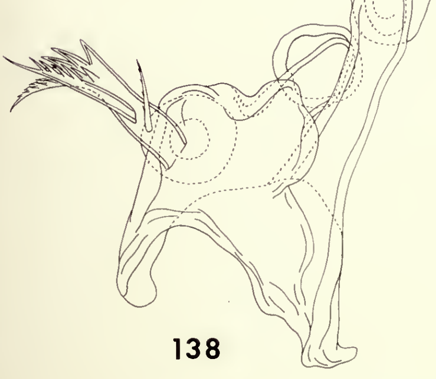
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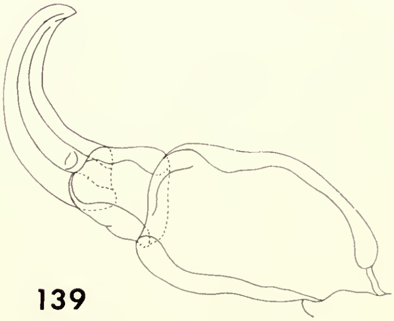
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THE CIRRIPED FAUNA OF TROPICAL WEST AFRICA

H. G. STUBBINGS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 15 No. 6
LONDON: 1967

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31 JUL 1967
NATURAL HISTORY

BY

H. G. STUBBINGS

Admiralty Materials Laboratory, Holton Heath, Poole

Pp. 227–319; 28 *Text-figures*, 1 *Plate*

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THE CIRRIPED FAUNA OF TROPICAL WEST AFRICA

By H. G. STUBBINGS

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SYNOPSIS

Sixty-nine species of Cirripedia are known from the tropical and warm-temperate waters of West Africa. This number includes littoral and shallow-water species and a very few from deep water. Further deep-water species, particularly of *Scalpellum* and *Verruca* may be expected when the deep basins off tropical West Africa are investigated more thoroughly. For this reason several species of Scalpellidae from the warm-temperate waters off north-west Africa, e.g. *Smilium longirostrum* (Gruvel) and *Scalpellum velutinum* Hoek, are included. The status of many rare or poorly recorded species requires further elucidation. The absence of the genus *Acasta* is remarkable.

The fauna contains elements from the north, *Scalpellum scalpellum* (L.) and *Chthamalus stellatus* (Poli) and from south-west Europe and the Mediterranean as would be expected from the published knowledge of the distribution of other groups of animals on this coast. Some of these species extend no farther south than Cape Verde, others extend to the south of the Gulf of Guinea. There is a very small South African component, of which *Chthamalus dentatus* Krauss is the most note-worthy. Four species, *Smilium renei* (Gruvel) *Chthamalus aestuarii* Stubbings, *Balanus pallidus* Darwin and *Chelonibia manati* Gruvel appear to be indigenous to tropical West Africa south of Cape Verde. The faunistic boundary in the region of Cape Verde noted by workers on other groups applies to many species of barnacle also.

I. INTRODUCTION

In considering the fauna of tropical West Africa it is appropriate to set limits to the region other than those imposed by the tropics of Cancer and Capricorn, to exclude those areas of coast, north and south, under the influence of the Canary and Benguela currents. Nicklès (1950) defined the " West Coast of Africa " for purposes of listing the Molluscan fauna, as the area between Cap Blanc in Mauretania and Mossamedes, Angola, that is approximately from 21° N. Lat. to 15° 30′ S. Lat. Longhurst (1962), reviewing the oceanography of the Gulf of Guinea has concluded that 14° N. and 14° S. Lat. present important faunistic boundaries corresponding to oceanographic frontal zones in these latitudes. These limits are in close agreement with those proposed by Ekman (1953) namely 15° N. and 15° S. (or possibly 16°–17° S.). This northern limit at 14–15° N. corresponds approximately to Cape Verde, Senegal, and there is evidence of a change of Cirriped fauna in this area, north temperate warm water species giving place to sub-tropical or tropical forms. In the present work Longhurst's (1962) limits of 14° N. and 14° S. are regarded as defining the tropical coast of West Africa but species from both farther north and south, which it seems likely may occur within these latitudes, have been included.

There is adequate material available from several sources linking the West African tropical fauna with that of the Atlantic north temperate zone. To the southward there is still a gap in our knowledge due to the virtual absence of information from south west Africa. In consequence the extent to which South African species penetrate northwards towards Angola is uncertain.

Broch (1924) summarized knowledge of the west African shallow-water barnacle fauna to that date. Few species had been recorded and many of the records gave vague localities, e.g. " West Africa ". Later works added only a little new informatin, but exploration since 1945 has increased our knowledge greatly. The " Atlantide " expedition, " Calypso " expeditions to the Gulf of Guinea and to the Cape Verde Archipelago and the Belgian Atlantique Sud expedition have all contributed. In addition collections made by the Museum d'Afrique Centrale (Tervuren), the Institut Français d'Afrique Noire, Dakar and the, now defunct, West African Fisheries Research Institute, Sierra Leone have all contributed specimens.

The present work reports on an extensive collection made in Ghana by Mr. R. Bassindale in 1949–51 and on a smaller one made by the author in Nigeria in 1957–8. Unpublished West African material in the British Museum is included. In order to make this report fully representative of the Cirriped fauna of the region, all species recorded by previous authors are included, provided the records are considered valid. The few species not included individually appear under the synonymy of species with which they have been merged since the original publication of the record. The species and varieties omitted are as follows :

> *Chthamalus stellatus depressus:* Nilsson-Cantell (1938), Gauld (1957), *C. cirratus:* Kolosvary (1941*b*, 1943*a*), *C. withersi:* and *C. rhizophorae:* Longhurst (1958) = *C. aestuarii* Stubbings.
>
> *Balanus amphitrite* var. *hawaiiensis:* Stubbings (1963) and *B. amphitrite* var. *denticulata:* Stubbings (1961*a*) = *B. amphitrite amphitrite* Darwin.
>
> *B. dybowskii* Gruvel (1903) and Broch (1924*a*), *B. amphitrite* var. *stutsburi* Darwin (1854) *et auct.*, *B. pallidus stutsburi:* Harding (1962) = *B. pallidus* Darwin.
>
> *B. dollfusi* Broch (1927) and Nilsson-Cantell (1938, 1939*b*) = *B. spongicola* Brown.
>
> *B. occidentalis* Stubbings (1961*a*, *b*) = *B. fallax* Broch.

It is probable that the littoral and shallow water Cirriped fauna of tropical Africa is now fairly well known and that few species remain to be discovered at least in the Lepadomorpha and Balanomorpha. There is still need for more information on the occurrence of the species of intermediate depths, i.e., of the continental shelf. The geographical range of *Scalpellum renei* Gruvel is uncertain and that of *Ibla atlantica* sp. n. virtually unknown. It is not improbable that intensive investigation of these intermediate depths will reveal further species.

Post-war investigations into the Acrothoracica have revealed several new West African species (Stubbings, 1961*b*, 1964*b*; Tomlinson, 1960) and there would appear to be a favourable field here for further work. The Ascothoracica have not been investigated so far. The considerable development of Zoanthid colonies in some areas, as on parts of the Ghana coast, would suggest the presence of these parasitic Cirripeds.

The deep-water fauna off the west coast of Africa has not been investigated to any extent. This is in marked contrast to the warm temperate region to the northward in which extensive work in the area of Madeira and the Azores has yielded many species notably of Scalpellum and Verruca (Aurivillius, 1898; Gruvel, 1900*a*, *b*). The German Tiefsee-Expedition made a number of stations down the coast in deep water from which which the deepwater *Scalpellids, Smilium longirostrum* and *Scalpellum trapezoideum*, were obtained (Weltner, 1922). As Gruvel (1905) could list 25 species of *Scalpellum* and 15 of *Verruca* from the northern warm temperate area it is probable that more species will be found when the deep waters of the Cape Verde, Sierra Leone, Guinea and Angola basins are worked systematically.

The following list of 70 species and varieties includes all those known to occur within the specified area plus a few that have been found outside it but may well be found there :

Mitella pollicipes (Gmelin)
Smilium longirostrum (Gruvel)
S. renei (Gruvel)
Scalpellum scalpellum (Linn.)
S. imperfectum Pilsbry
S. trapezoideum Hoek
S. velutinum Hoek
Ibla atlantica sp. n.
Lepas anatifera Linn.
L. anserifera Linn.
L. hillii Leach
L. fascicularis Ellis and Solander
L. pectinata Spengler
Heteralepas cornuta (Darwin)
Paralepas minuta (Philippi)
Conchoderma auritum (Linn.)
C. virgatum (Spengler)
C. virgatum var. *chelonophilum* Leach
Trilasmis (*Poecilasma*) *crassum* (Gray)
T. (*P.*) *kaempferi* (Darwin)
Octolasmis tridens (Aurivillius)
O. lowei (Darwin)
O. hoeki (Stebbing)
Verruca striata Gruvel
Chthamalus stellatus stellatus (Poli)
C. stellatus bisinuatus Pilsbry
C. dentatus Krauss
C. aestuarii Stubbings
C. fragilis Darwin
Pachylasma giganteum (Philippi)
Balanus (*Megabalanus*) *tintinnabulum tintinnabulum* Linn.
B. (*M.*) *tintinnabulum maroccana* Broch
B. (*M.*) *tintinnabulum zebra* Darwin
B. (*M.*) *tintinnabulum concinnus* Darwin
B. (*M.*) *tintinnabulum spinosus* (Gmelin)
B. (*M.*) *tulipiformis* Darwin
B. (*M.*) *nigrescens* Lamarck
B. (*M.*) *maxillaris* (Gronovius)
B. (*Balanus*) *trigonus* Darwin
B. (*B.*) *spongicola* Brown
B. (*B.*) *perforatus* Brug.
B. (*B.*) *perforatus* var. *angustus* Gmelin
B. (*B.*) *perforatus* var. *fistulosus* Poli
B. (*B.*) *eburneus* Gould
B. (*B.*) *improvisus* Darwin
B. (*B.*) *improvisus* var. *assimilis* Darwin
B. (*B.*) *amphitrite amphitrite* Darwin
B. (*B.*) *amphitrite albicostatus* Pilsbry
B. (*B.*) *pallidus* Darwin

B. (*B.*) *venustus venustus* Darwin
B. (*B.*) *venustus niveus* Darwin
B. (*Hesperibalanus*) *fallax* Broch
B. (*Conopea*) *calceolus* Darwin
Tetraclita divisa Nilsson-Cantell
T. purpurascens Wood
T. squamosa squamosa (Brug.)
Pyrgoma anglicum Sowerby
Chelonibia testudinaria Ellis
C. caretta Spengler
C. manati Gruvel
C. patula (Ranzani)
Coronula complanata (Mörch)
Platylepas hexastylos (O. Fabr.)
Stomatolepas elegans (O. G. Costa)
Xenobalanus globicipitis Steenstrup
Cryptophialus coronatus Tomlinson
C. variabilis Stubbings
Kochlorine hamata Noll
K. inermis Stubbings
Kochlorinopsis discoporellae gen. et. sp. n.

References under species synonymy have been reduced to as few as possible and are only given when the species is but little known, though originally described long ago, e.g. *Smilium renei* (Gruvel, 1902) or when the nomenclature is questioned or has been recently, e.g. *Chthamalus aestuarii* Stubbings, 1963. References to geographical distribution are given only in the text.

Locality citations for material reported here for the first time are arranged geographically according to country of origin from North Africa to the Cape. Mr. Bassindale carried out a large number of trawl and dredge hauls in a circumscribed area off Accra, Ghana, in addition to collecting at many named shore localities. The Accra stations are referred to here by their numbers. For full available details of these collecting stations reference should be made to Bassindale (1961).

Mr. Bassindale's material comprises the largest part of that described here. To avoid excessive repetition his name does not appear in the locality citations. Other sources of materials are distinguished by citation of the collecter's name and where appropriate the British Museum registration number. The author's own collections are followed by his initials (H.G.S.) with or without a serial collector's number as appropriate. Samples collected by the Staff of the Tropical Testing Establishment of the Ministry of Supply in 1953–4 are designated by the initials T.T.E.

The " dolphin " mentioned in some references to Port Harcourt, Nigeria, is a concrete structure erected in the river to aid in warping out ships from the quay but no longer used.

2. SYSTEMATIC ACCOUNT

LEPADOMORPHA

MITELLA

Mitella pollicipes (Gmelin)

Mitella pollicipes: Stubbings, 1965, 877.

LOCALITIES: Cape Verde Is.: (1) St. Vincent, coll. Mrs. M. G. Bannerman. (2 spec.) B.M. 1915.1.11.1–2. (2) coll. C. R. Stonor. B.M. 1939.7.22.9–13 (21 large and 6 small spec.).

The distribution of *M. pollicipes* is rather clearly defined. On the European Atlantic coast it is found from Finisterre to Spain and Portugal (Bishop *et al.*, 1957 ; Gruvel, 1920 ; Fischer-Piette & Prenant, 1956, 1957). In the Mediterranean, Llabador (1937) has established its occurrence on the Algerian coast from Algiers westward. From the northern shore there is a doubtful reference to the species from Nice (Caziot, 1921) based on a century-old record of Verany (1862) but it is not recorded from Banyuls (Utinomi, 1959*a*). Kolosvary (1940) records it from the Mediterranean without precise locality. Most recently Barnes & Barnes (1964 : 9) record it from Catalan Bay, Gibraltar. The textual name *polymerus* in this paper is a MS error (Auct. in litt.).

From Algeria it extends westward and southward on the African coastline and is found in suitable situations in Morocco, Rio de Oro, Mauretania and Senegal (Broch, 1927*a* ; Gruvel, 1912 ; Nilsson-Cantell, 1939*b* ; Stubbings 1965). Sourie (1954) states that it is well represented at Dakar and fairly common at Cap Blanc (Mauretania). He did not find it at Conakry, French Guinea and there seems no doubt that Dakar defines the southern limit of the species in West Africa.

From the Atlantic islands there are very few records. The above noted material in the British Museum confirms the presence of *M. pollicipes* in the Cape Verde archipelago. Its absence from the " Calypso " Cape Verde collections (Stubbings, 1964*a*) suggests, however, that it is not very common there. From the Canary Is. there are no recent records, but Darwin (1851) clearly handled material from Teneriffe. Its presence, or absence, in the Azores likewise needs elucidation. Weltner (1897) records specimens from " Portugal oder Acoren " but there is no certain record from these islands.

The inclusion of England, Scotland, Ireland, the North Sea and even Jan Mayen within the area of distribution of *M. pollicipes* (Darwin, 1851 ; Weltner, 1897 ; Gruvel, 1905) would seem highly improbable except for chance specimens on drift, an unusual habitat for the surf-loving *Mitella*. The Indonesian record of Tonkin (Gruvel, 1912) likewise is improbable.

Smilium renei (Gruvel)

Scalpellum renei Gruvel, 1902*b*, 229–233, pl. 12, figs. 5–7.
Scalpellum (*Smilium*) *renei:* Pilsbry, 1907, 13.
Smilium renei: Stubbings, 1961*a*, 9–11, text-fig. 1.
Smilium renei: Stubbings, 1961*b*, 181.

LOCALITY : Ghana : Off Accra Sta. 72, 38m, on fine branches of an Alcyonarian (2 spec.).

One specimen measured, capitulum 3·0 mm., peduncle 1·5 mm., and the other capitulum 2·0 mm., peduncle 0·75 mm. These are small compared with Gruvel's type specimen which has capitular and peduncular lengths each 5·25 mm., and the largest Atlantide specimens which had a capitular length of about 7·0 mm.

The species has now been recorded from French Guinea, Ivory Coast, Ghana, Nigeria and Angola, thus establishing its presence as a shallow-water species throughout tropical West Africa from approximately 10° N. to 10° S. Lat.

Smilium longirostrum (Gruvel)

Weltner (1922) records this species in 2480 m. south of the Canary Islands, Lat. 24° 35′ N., Long 17° 4′ W., i.e., somewhat to the north of the area under discussion. It is thus a species that may be expected to occur in the deep water basins off tropical West Africa.

Scalpellum scalpellum (Linn.)

Localities: (1) Gambia, on carapace of the crab *Acanthocarpus africanus*, coll. A. R. Longhurst, B.M. 1956.1.7.1.(1 spec.); (2) Sierra Leone, W.A.F.R.I. sta. MB1/A4, on continental shelf 88 m., on a spine of *Cidaris cidaris meridionalis*, coll. A. R. Longhurst, B.M. 1956.4.27.1.(1 small spec.).

The southward distribution of *Sc. scalpellum* in coastal waters of the sub-tropical and tropical eastern Atlantic is now fully documented. It has been reported from the western Mediterranean (Utinomi, 1959*a*, *b*) and Adriatic (Broch, 1953*b*), Morocco and Rio de Oro (Broch, 1927*a*; Gruvel, 1902*a*), Canary Is. (Gruvel, 1920), Cape Verde Is. (Stubbings, 1964*a*), Senegal and Gambia (Stubbings, 1965), Sierra Leone (Stubbings, 1961*a*), Nigeria (Stubbings, 1961*b*), Gabon and the Congo estuary (Stubbings, 1963). This species is now known to have a vast range in latitude from Iceland and Lofoten, Norway (Lat. 68° N.) (Broch, 1924*c*) to the Congo (Lat. 6° S.).

Scalpellum imperfectum Pilsbry

Scalpellum imperfectum Pilsbry, 1907, 75–77, pl. 4, figs. 15–18, text-fig. 30.
Scalpellum imperfectum: Stubbings, 1961*a*, 11–13, text-fig. 2.

Not represented in the Ghanaian and Nigerian collections. The few records of this species indicate a very wide geographical range. In the Atlantic there are three records from eastern North America (Pilsbry, 1907), one from south of Iceland (Broch, 1953*a*), one from off Spanish Guinea (Stubbings, 1961*a*) and one from the Cape (Barnard, 1924). There is a further record from the Galapagos Is. (Macdonald, 1929).

Scalpellum trapezoideum Hoek

A single specimen of this species is recorded by Weltner (1922) from the Bight of Biafra in 2492 m. Lat. 2° N. Long. 8° 4′ E. It remains the single deep water species recorded from tropical West Africa as here defined.

Scalpellum velutinum Hoek

Scalpellum velutinum has not been found within the area but the "Talisman" took it in 882 m. off Pilones, Rio de Oro, as well as at two stations in Morocco and at Fuerteventura, Canary Islands (Gruvel, 1902*a*). It is, therefore, to be expected that *S. velutinum* will be found in the deep basins south of Cape Verde.

Ibla atlantica sp. n.

LOCALITY: Sierra Leone: (1) W.A.F.R.I. Sta. MB1/B4, 08° 45′ N., 14° 38′ W., 220–440 m. (1 spec.): Sta. MB1/B5, same position, 800 m. in burrows of *Pholadidea* prox. *loscombiana* Turton (Lamell., Pholadidae) (3 spec.).

DIAGNOSIS: Unisexual: female with peduncle clothed in golden spines; opercular valves golden brown with prominent growth ridges: no male organs: caudal appendages minute, one-segmented: cirri with numerous segments, increasing in number from C1 to C6. Male differentiated into peduncle and capitulum, attached to mantle wall by the antennae.

TYPE LOCALITY: as above, Guinea shelf off Sierra Leone, West Africa (see Longhurst, 1958, p. 73 and text-fig. 2). Holotype in British Museum B.M. 1956.4.27.3, a specimen with long peduncle from sta. MB1/B5: paratypes: 1) 2 other specimens from MB1/B5, one dissected registered number B.M. 1956.4.27.4. and slides reg. no. B.M. 1956.4.27.6 and 2) 1 specimen from sta. MB1/B4, reg. no. B.M. 1956.4.27.5.

FEMALE: Valves golden brown with prominent growth ridges: scutum curved slightly towards tergum, the occludent margin slightly convex. Peduncle paler in colour, densely clothed in short golden hairs curved towards the valves. Length of peduncle variable, the lower portion narrowed and embedded in the wall of the mollusc burrow. Size 9·5 (5·0) mm. (MB1/B4); 14·5 (4·0) (Text-fig. 1*a*), 8·5 (3·5)

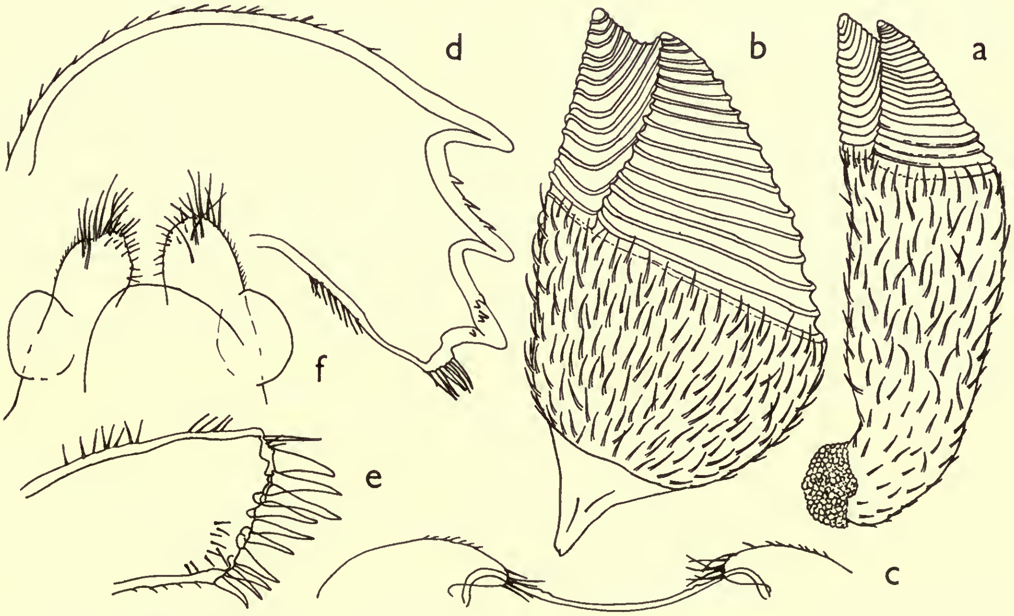


FIG. 1. *Ibla atlantica* sp. n.: *a*, type specimen, 14·5 mm. overall, with long peduncle (x c. 5); *b*, paratype, 8·5 mm. overall from same haul (×8·5); *c*, labrum (×47); *d*, mandible; *e*, maxilla I (both ×135); *f*, paired maxilla II (×47).

(Text-fig. 1*b*) and 6·5 (3·0) mm. (MB1/B5) overall. Figures in brackets are the respective lengths of the valves.

Labrum (Text-fig. 1*c*) smoothly concave without teeth or hairs on margin. The palps are small, oval with a few short terminal setae. The mandible (Text-fig. 1*d*), bears denticles on the upper margin of the second and third teeth. The lower angle carries a tuft of short stout setae. The first maxilla (Text-fig. 1*e*) has a convex margin with ten stout spines. Maxilla II (Text-fig. 1*f*) has rather short terminal setae and very short setae on both inner and outer margins. The lower lobe is almost as large as the main lobe. The two appendages are set wide apart and there is a raised fold posterior to them " closing the gap " as described by Darwin.

The cirri have short segments rather broader than long near the base but elongating somewhat distally. There are one or two setae distally on the posterior margin. On the anterior margin each segment bears one pair of large setae distally with a single fine seta beside or between them. A smaller, often very small, pair of setae lies below the main pair. The number of segments in the cirri is high :

Cirrus	I	II	III	IV	V	VI
Segments	14·22	27·31	36·35	35·37	39·39	40·42

The caudal appendages are minute consisting of one oval lobe less than half the length of the pedicel of cirrus VI.

The mantle cavity contained nine minute individuals all apparently attached to the mantle wall, though six of them were early embryos. Two embryos had a single well-developed pigmented eye (? nauplii) and only one was recognizable as a young male probably recently metamorphosed as the single eye was still visible.

The male has clearly differentiated capitulum and peduncle and is attached by the antennae embedded in a mass of cement in the mantle wall. The black nauplius eye is still visible. The lobes of the cement gland are clearly visible within the capitulum and adjacent to the peduncle. The prosoma was poorly preserved and did not stain well. Little can be made out but an elongated slightly dumb-bell shaped structure, staining deeply probably represents the vesicula seminalis and male reproductive organs. The portion towards the base of the capitulum may be double, the two lobes lying one over the other, in which case two testes are present. This structure is obscured further by the presence of the cement gland. No valves are discernible.

Including *Ibla atlantica*, five species of *Ibla* are now recognized namely,

I. quadrivalvis Cuvier 1817
I. cumingi Darwin 1851
I. segmentata (Studer 1889)
  syn. *I. pygmaea* Broch 1922
I. idiotica Batham 1945
I. atlantica sp. n.

Two of these species, *I. quadrivalvis* and *I. segmentata* are hermaphrodite. *I. quadrivalvis* has extremely long caudal appendages composed of 32 segments and up to three-quarters the length of the rami of cirrus VI. *I. segmentata* has fairly long caudal appendages of about 10 segments, longer than the pedicel of cirrus VI. Of the other three, female, forms without penis, only *I. cumingi* has long caudal appendages. *I. idiotica* resembles the new species in the minute caudal appendages, but differs in having only a few segments, up to 8, in the short rami of the cirri and in its very small size. There is no doubt that *I. atlantica* represents a new species of *Ibla*.

This is the first record of the genus from the Atlantic ocean. Although many records of *Ibla* spp. note the association with larger Cirripedia (Batham, 1945; Newman, 1960) this association has been shown not to be obligatory. The occurrence of Ibla in the burrows of an unrelated organism, as here, seems to be a hitherto unrecorded phenomenon.

Lepas anatifera Linn.

Lepas anatifera: Gauld, 1957, 10.
Lepas anatifera: Stubbings, 1961*a*, 13–14.

Not represented in the Ghanaian and Nigerian collections.

This species was collected from the hull of the Danish Expedition ship " Atlantide " at ports in Liberia, Ghana and Nigeria (Stubbings, 1961*a*). The duration of the ship's stay in West African waters, six weeks before the earliest of these collections, leaves no room for doubt that *L. anatifera* is present in those waters and was not brought from further north by the ship. There are few other records from the west coast. Gauld (1957) records this species from beaches in Ghana and Weltner (1897) specimens from the Cameroons. Evans (1958) has discussed the growth rate of specimens on the hull of " Petula " which must have settled in the vicinity of the Cape Verde Is.

From further north there are records by Gruvel (1920) and Broch (1927*a*) from Morocco. There are many records from the Azores (Gruvel, 1920). The British Museum has recent material from the Azores (B.M. 1955.9.2.2–3, coll. G. Chapman) and from Funchal, Madeira (B.M. 1954.9.15.4 coll. D. W. Tucker). *L. anatifera* is much less common on the West Coast than *L. anserifera* and from the greater number of records from more temperate waters it is possible that *L. anatifera* prefers rather lower temperatures than obtain in the tropical Eastern Atlantic.

Lepas anserifera Linn. 1767

Lepas anserifera : Gruvel 1912, 344–345.
Lepas anserifera : Broch 1924*a*, 202.
Lepas anserifera : Stubbings 1961*a*, 14; 1963, 4–5; 1964*a*, 104; 1964*b*, 330.

LOCALITIES: (1) Sierra Leone, on a floating plant stalk, —.2.55, coll. A. R. Longhurst, B.M. 1956.1.7.2 (28 almost full-grown spec.); (2) " off West Africa ", coll. A. R. Longhurst, B.M. 1957.6.3.2 (3 part-grown spec.).

Ghana: (1) Accra, on cuttlefish " bone ", 1935 coll. F. R. Irvine (5 spec.); (2) Takoradi, coll. Mrs. Carlyle Bell, B.M. 1948.1.17.1 (1 spec.); (3) Takoradi, on floating seeds, 6.1.55, coll. D. T. Gauld (5 spec.); (4) Prampram, —.11.37, coll. Miss V. J. Foote, B.M. 1952.5.7.1 (many very small spec.); (5) Senegal, on *Sargassum* coll. Captain Moloney, B.M. 85–5 (9 small spec.).

Nigeria, Lagos: (1) on cuttlefish " bone " coll. Miss E. Trewavas, B.M. 1948.3.20.1 (27 nearly full grown spec. and some very small ones); (2) coll. Captain Moloney, B.M. 91.4.1.59–63 (10 large and 12 very small spec.).

Cameroons: (1) Off Fernando Po. coll. R. C. Ward, B.M. 1962.4.17.1 (34 spec.); (2) Debunscha Beach, Victoria, from a log 21.5.61, coll. J. T. Swarbrick, B.M. 1962.8.1.1 (about 90 spec. in small clusters).

Specimens in each of these collections have been checked for the possession of five filamentary appendages. The Debunscha beach specimens are of interest in respect of the very white shells with no bluish shadowing from the pigmented mantle and for the deep orange colour of the edge of the mantle.

In addition to the authors cited above, Weltner (1897) and Nilsson-Cantell (1921) record *L. anserifera* from the Cameroons. It is evidently the most widely distributed and frequently occurring species of *Lepas* in Tropical West Africa.

Weltner (1897) records " *L. pectinata* Spengler var. Darwin " from " West Africa " and Brian and Dartevelle (1954) record *L. pectinata* from Moita Seca at the mouth of the R. Congo. As reported elsewhere (Stubbings 1964*b*) I can find no *L. pectinata* in Dr. Dartevelle's material from Congo that I have examined all of which appears to be *L. anserifera*.

Lepas hillii (Leach) 1818

Locality: Ghana, Tenpobo: on cuttlefish " bone ", 1.2.50, coll. R.Bassindale (many small spec.).

These specimens, preserved in Bouins fluid, were completely decalcified and spoiled. From the presence of three filamentary appendages, a pair at the base of cirrus I and a single one on the prosoma, and apparently a gap between carina and scutum, they have been referred to *L. hillii*.

The above specimens appear to be the only ones recorded from the West African *coast*. Evans (1958) recorded them on the hull of " Petula " and deduced that they must have settled there shortly after the vessel left Dakar. They may be presumed to have settled during the voyage between that port and the Cape Verde Is. Hoek's (1883) specimens taken from the screw of H.M.S. " Challenger " at St. Vincent, Cape Verde Is. and those removed from " Atlantide " in Le Havre (Stubbings, 1961*a*) have a less certain provenance. Specimens have been taken off Morocco (Aguilar-Amat, 1927) and at Tangier (Gruvel, 1912) and many off the Azores (Gruvel, 1907*b*, 1920) and in the W. Mediterranean (Utinomi, 1959*a*). *L. hillii* is thus distributed over the eastern tropical and sub-tropical North Atlantic, but evidently rather few specimens occur in-shore. It is not represented in the collections of the Institut Français d'Afrique Noire in Dakar or in those of the Musée Royal de l'Afrique Centrale, Tervuren.

Lepas pectinata Spengler

non *Lepas pectinata*: Brian & Dartevelle 1954, 150.

There is no reliable evidence of the occurrence of *Lepas pectinata* on the tropical West African coast. The only precise record in the literature is that of Brian and Dartevelle (1954) from the Congo estuary which the author has given reasons for referring to *L. anserifera* (Stubbings 1964*b*). Weltner (1897) recorded the " var. Darwin " from W. Africa without precise locality. Further, Gruvel (1907*a*) recorded the species from " West of the coast of Guinea " and (1910) gave the same locality statement and also Porto Grande, St. Vincent, C. Verde Archipelago. The author has seen no material in the several collections handled that is referrable to *L. pectinata* and so considers it at best a doubtfully West African form. In 1966 R.R.S. " Discovery " took some recently metamorphosed *Lepas* off Fuerteventura, Canary Islands. These can be assigned with some degree of confidence to *L. pectinata*. Thus, after a lapse of over 50 years reliable *L. pectinata* material has been obtained from the eastern Atlantic. There is a reasonable possibility, therefore, that it will be found sooner or later in inshore or estuarine waters of tropical West Africa.

Lepas fascicularis Ellis and Solander

Not represented in the Ghanaian and Nigerian collections.

The paucity of records of *L. fascicularis* from the west coast has been noted (Stubbings, 1965). That so few specimens are contained in the Institut Français d'Afrique Noire, in Dakar can only indicate its infrequent occurrence in the Senegal area. Its scarcity on the Ghana coast and off Sierra Leone must be presumed for the same reasons. It has been recorded once from Morocco (Broch, 1927*a*) and once west of the Canary Islands (Gruvel, 1920). Available evidence thus suggests that *L. fascicularis* is not common on the north-west coast or west coast north of the equator. Its apparent abundance off the Congo estuary (Stubbings, 1963) is in complete contrast.

Heteralepas cornuta (Darwin)

Not represented in the Ghanaian and Nigerian collections.

The distribution of *H. cornuta* is still very imperfectly known. The records given by Broch (1927*a*) and Stubbings (1964*a*, 1965) suggest that it is present over a wide area of the north-western part of the coast of West Africa from the mouth of the Mediterranean to Cape Verde and the Cape Verde Archipelago. As it was not represented in collections from Ghana, Nigeria, the Gulf of Guinea, the Congo estuary and Angola it may well be that it is absent south of Cape Verde. This, however, would be surprising in view of its occurrence much further afield in the West Indies (Darwin, 1851) and the Andaman Sea (Nilsson-Cantell, 1938*a*). *H. cornuta* is apparently a deep-water species, all records being from below 100 m. and one at least from 750 m., so the lack of records from the tropical and southern subtropical coasts of West Africa may be due to the comparatively small number of deep-water collections so far made there.

Paralepas minuta (Philippi)

LOCALITY : Sierra Leone : (1), W.A.F.R.I. Sta. MBI/A5, 132 m., 22.2.56, from near base of primary spines of *Cidaris cidaris meridionalis* B.M. 1956.4.27.2 : (2) the same, B.M. 1956.4.27.2A. (33 juv. spec.).

The recorded localities for *P. minuta* were listed by Stubbings (1961*b*). It occurs from Sicily in the central Mediterranean westwards to Gibraltar and down the African coast as far as Liberia (4° 40′ N.), the most southerly record being that made by the " Gazelle " (Studer, 1882, 1889). According to Broch (1927*a*) it occurs also in Madeira. The geographical distribution of *P. minuta* off north-west Africa is, therefore, somewhat greater than that of *H. cornuta* which is as yet unknown from the Mediterranean or from south of Cape Verde.

Conchoderma auritum (Linn.)

Not represented in the Ghanaian or Nigerian collections, *C. auritum* has been recorded from West African waters by Gruvel (1910), Weltner (1922), Kolosvary (1943*a*) and Stubbings (1961*a*). Three of these reports record material from a ship's hull, the fourth (Kolosvary, 1943*a*) from a whale. Where precisely in tropical Atlantic waters settlement occurred cannot be determined. Broch (1924*a*, 1927*a*) summarized the then known occurrence of the species in the tropical and sub-tropical Atlantic but added no new localities. As there are records from the Mediterranean (Monod, 1938 ; Nilsson-Cantell, 1932*a*) and South Africa (Barnard, 1924 ; Nilsson-Cantell, 1930*a*) and from off-shore West African waters (Weltner, 1887) a general distribution of this pelagic species in warm-temperate and tropical eastern Atlantic waters may be presumed.

Conchoderma virgatum (Spengler)

LOCALITY : Madeira, Funchal, 12 juv., Aug. 1953, coll. D. W. Tucker, B.M. 1954.9.15.2 (12 juv. spec.). Not represented in the collections from Ghana and Nigeria.

Records of this cosmopolitan species refer almost entirely to specimens recovered from the hulls of ships either in tropical or warm temperate waters or shortly after moving into cooler waters. The major exception is that series of specimens collected mainly from fishes at Gorée, Senegal in the collection of I.F.A.N., Dakar (Stubbings, 1965).

Records north of the equator range from 2° N. (Nilsson-Cantell, 1930*a*) to nearly 42° N. (Gruvel, 1920). South of the equator there are fewer records except for South Africa (Barnard, 1924, 1925). It may be expected anywhere off the West African coast where flotsam comes ashore or craft are moored or ply for long periods in warm waters.

var. ***chelonophilum*** Leach

Not represented in the collections from West Africa.

There are a number of records from the Atlantic in Lat. 30°–40° N. (Hoek, 1883 ; Leach, 1818 ; Weltner, 1897 ; Gruvel, 1920) and Chevreux and de Guerne (1893) have recorded it from the western Mediterranean. The specimens reported by

Stubbings (1961*a*) were very small and could also have come from these warm temperate waters and not from tropical West African waters. Accordingly, the presence of this variety in West African waters requires confirmation.

Trilasmis* (*Poecilasma*) *crassum (Gray)

Weltner (1922) records this species from Grosse Fischbai (= Tiger Bay), Angola. As it was originally described from Madeira (Darwin, 1851) it is conceivable that it may yet be found within the report area.

Trilasmis* (*Poecilasma*) *kaempferi (Darwin)

Not represented in the Ghanaian and Nigerian collections.

There are numerous records of this species from the warmer North Atlantic, particularly from the region of the Azores (Gruvel, 1902*b*, 1920). It is also known from Madeira (Darwin, 1854, Weltner, 1897). From the West Coast of Africa there are comparatively few records: from Cape Bojador, Morocco (Gruvel, 1902*a*), Senegal (Stubbings, 1965); Spanish Guinea (Stubbings, 1961*a*) and in the South Atlantic from Grosse Fischbai (Weltner, 1922). Barnard (1924) records the species from Cape Point and off the Buffalo River, South Africa. *T.* (*P.*) *kaempferi* is therefore widely distributed in the eastern Atlantic at depths of 100 to 1,500 m. and can be expected off the West African coast wherever local conditions are favourable.

Octolasmis tridens (Aurivillius)

The only record of this species from West Africa is that from the Cape Verde Islands collected by the Danish "Atlantide" Expedition (Stubbings, 1961*a*). About 100 specimens of *O. tridens* were found on that occasion on a single Palinurid crawfish, yet no other specimens seem to have been collected from either the Islands or the African mainland.

Octolasmis lowei (Darwin) 1851

LOCALITIES: Mauretania: Cap Blanc, on gills of a crab, coll. M.H. Routh, B.M. 1952.10.2.7 (many spec.).

Ghana: (1) Accra, on the Crab *Callinects gladiator* coll. D. J. Gauld (28 spec.); (2) off Chorkor, on gills and in branchial chamber of the crab *Apiomithrax bocagei* (Osorio) (numerous spec.); (3) off Chorkor, in branchial cavity of *Calappa rubroguttata* Herklots (1 spec.).

The largest Ghanaian specimen had a capitular length of 2·5 mm. and a peduncle of 3·0 mm. A number contained developing eggs. The species was described by Darwin from Madeira and is recorded by Broch (1924*b*) from Mauretania and by Brian & Dartevelle (1954) from Luanda, Angola. It is evidently distributed over both the tropical and subtropical West African coast-line.

Gauld (1957) records *D. lowei* from *Callinectes gladiator* and has found it also on species of *Neptunus*, *Cronius*, *Micropisa*, *Dromia* and *Palinurus* (Buchanan, 1958: 23). Brian & Dartevelle (1954) cite also *Echinoplax* and *Maia*. The presence of a single specimen of *O. lowei* in the branchial space of *Calappa rubroguttata* is noteworthy as Gauld states that this crab is the only one examined by him in large numbers without finding this cirripede. A number of *Callinectes* collected at Port Harcourt were quite free from *Octolasmis*, perhaps due to the lowered salinity, which may fall to only 12‰ in the wet season.

Octolasmis hoeki (Stebbing)

Dichelaspis hoeki Stebbing, 1895, 18–19, pl. II, figs. A–D.
non *Dichelaspis antiguae* Stebbing, 1895, 19–20, pl. II, figs. E–G.
Octolasmis hoeki: Nilsson-Cantell, 1927, 763–6, text-fig. 9.

LOCALITY : Ghana, Tema ; on *Scyllarides* sp. 2.9.59, coll. D. T. Gauld (11 spec.).

A suggestion from Mr. W. A. Newman of the Scripps Institution to the effect that some *O. hoeki* from Cape Verde Is. (Stubbings, 1964*a*) were probably not this species on the grounds of differences in mouth appendages, prompted a re-examination of Stebbing's types of *D. hoeki* and *D. antiguae.* Stebbing (1895) described the two species from material from Antigua, W.I., and listed a number of points in which they differed, both in valve form and internal morphology. His figures are, unfortunately, inadequate. Annandale (1910 : 217) studying further West Indian material admitted the occurrence of these differences, but found they were not correlated one with the other and united Stebbing's two species under *D. hoeki* which has page priority. Nilsson-Cantell (1927) was of the opinion that too much emphasis had been laid on differences in valve form in *Octolasmis* and followed Annandale, at the same time including *D. aurivillii* (Gruvel, 1902*b*) as a further synonym. He did not consider the differences in number of segments in the cirri of the two forms to be significant. Neither were the even smaller differences in caudal appendages considered of sufficient importance to justify the maintenance of the three species. Nilsson-Cantell (1927) does not mention the difference in setation of the segments noted by Stebbing. This was unfortunate as there seems here to be a constant difference between *O. hoeki* and *O. antiguae.*

In order to clarify the position, specimens variously named *Dichelaspis*, or *Octolasmis*, *hoeki* and *antiguae* from the West Indies, Cape Verde Islands and West Africa have been examined. They are referable to one species or the other and will be discussed below under these two species headings.

MATERIALS EXAMINED : Tema, Ghana, W. Africa, coll. D. T. Gauld ; Cape Verde Islands (" Calypso " Exped. 1959 : Stubbings 1964*a*) ; Cape Verde Islands (B.M. 79–10 : publ. Nilsson-Cantell 1927) ; Dry Tortugas, W. Indies (B.M. 1952.6.10.2) ; Antigua, W. Indies (B.M. 1928.12.1.2988–2993, syntypes).

The shape of the opercular plates has been considered in some detail by Nilsson-Cantell (1927). He concluded that the differences between scutum and tergum in *O. hoeki* and in *O. antiguae,* described by Stebbing, were merely variations associated with age. The shape of these valves does, undoubtedly, vary with age as does also the proportion of the capitulum covered by the valves. Text-fig. 3 shows the scutum and tergum of a series of specimens of increasing capitular length from 2·03 to 3·44 mm. from Tema, Ghana. The gap between base of tergum and scutum becomes proportionately greater as the capitulum increases in size. The Cape Verde material (B.M. 79–10) shows a similar proportional reduction in the area covered by the valves.

Particular regard should be paid to the shape of the tergum (Text-figs. 2*a*, 3).

Owing to the deep emargination of the scutal margin of the tergum to accommodate the occludent lobe of the scutum the basi-occludent angle of the tergum has a "hooked" or "beaked" appearance. Also, the portion of the scutal margin opposite the basal segment of the scutum is marked off distinctly from the remainder so that a distinct corner is produced on the valve at this point. This angle is marked equally clearly in young and old specimens. The sharpness of the angle varies considerably.

The appendages have been compared in specimens from Stebbing's syntypes (Text-fig. 2*b–e*), from Tema (Text-fig. 4*a–e*) from the Cape Verde Islands and from the Tortugas. These may be compared with the published illustrations of the Cape

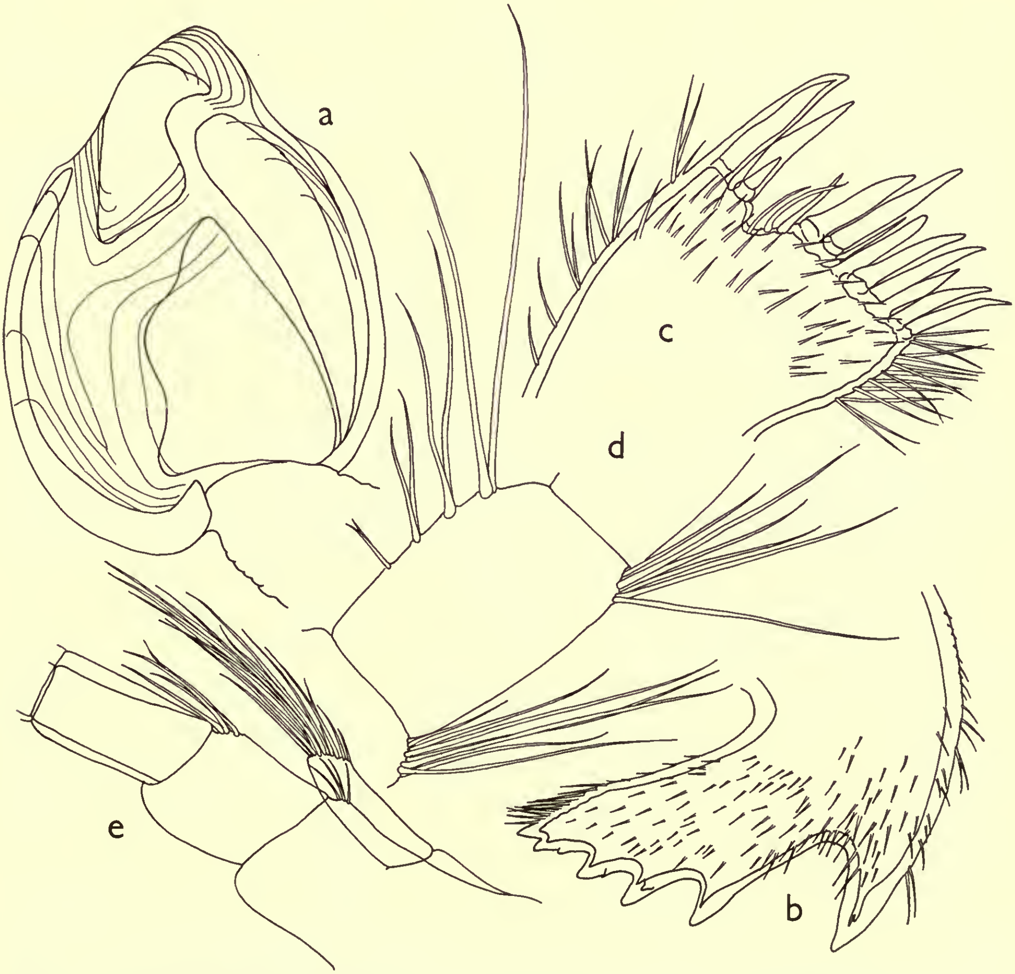


Fig. 2. *Octolasmis hoeki* (Stebbing) : syntype (B.M. 1928.12.1) : *a*, whole animal (×20) ; *b*, mandible (×183) ; *c*, maxilla I (×300) ; *d*, segment 4 of posterior ramus of cirrus VI (×205) ; *e*, base of cirrus VI and caudal appendages (×100).

Verde material (Nilsson-Cantell, 1927) and the author (1964*a*) and also with Stebbing's (1895) rather inadequate figures. They are all very similar and referable to the same species, *O. hoeki* (Stebbing). The following points are noteworthy: The mandible (Text-figs. 2*b*, 4*a*) has fourteeth, the third and fourth, and sometimes the second, with a subsidiary cusp. The lower angle is produced into two acute teeth, the upper of which has a subsidiary cusp. All the subsidiary cusps are weakly developed. The first maxilla (Text-figs. 2*c*, 4*b*) has two large spines above the notch with a third

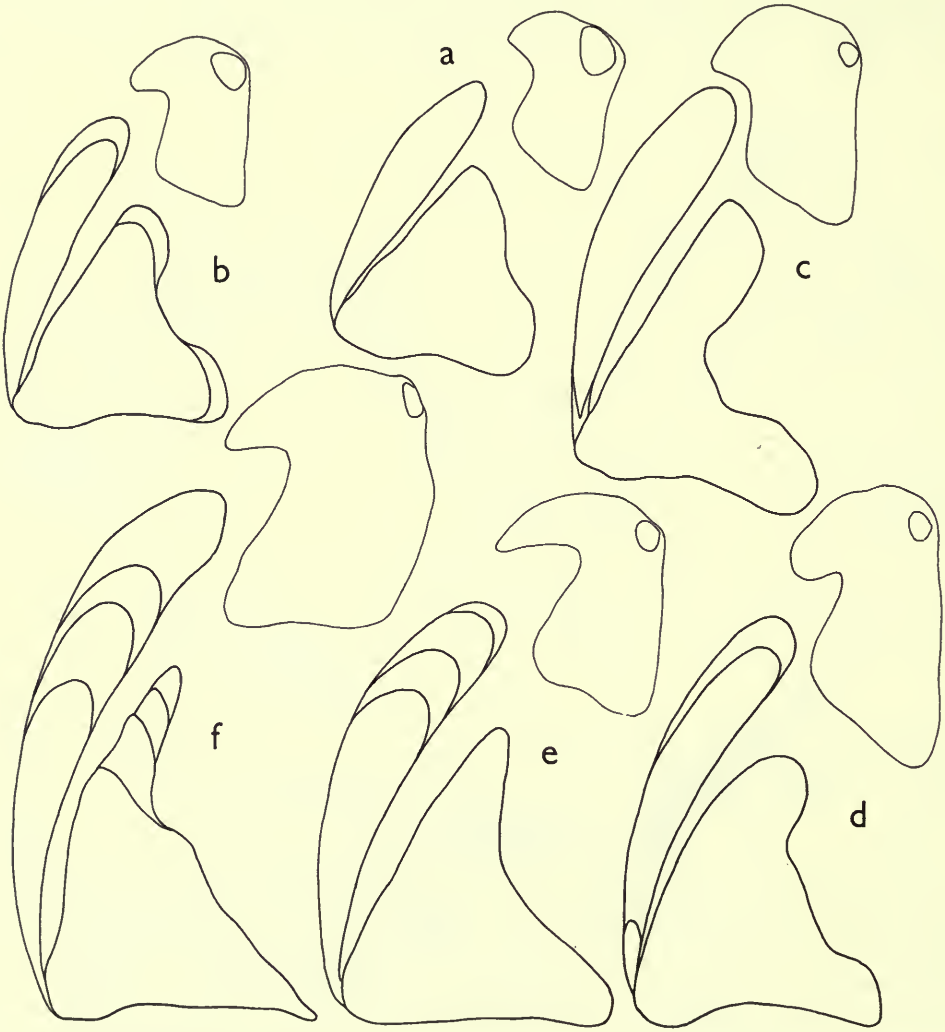


Fig. 3. *Octolasmis hoeki* (Stebbing): right scutum and tergum of specimens of increasing size from Tema, Ghana to show change in shape of valves and in proportion of capitulum covered: capitular lengths *a*, 2·03 mm., *b*, 2·09 mm., *c*, 2·71 mm., *d*, 2·89 mm., *e*, 3·01 mm., *f*, 3·44 mm.

smaller spine lateral to the second spine. This third spine has not been reported hitherto. The notch is distinct and fairly deep. About three stout setae project from the notch. The lower part of the maxilla stands a little forward of the upper part. It bears a variable number of stout spines, eight or nine in those figured. Nilsson-Cantell (1927, Text-fig. 9*c*) shows only six. The second maxilla (Text-fig. 4*c*) is rounded with the front edge more or less flattened with spines along the whole border, as described and figured by Nilsson-Cantell (1927, Text-fig. 9*d*).

The number of segments in cirri II–VI varies between 8 and 12, the average falling between 9 and 10 for both rami. The numbers found in specimens from several localities and reported in the literature or newly examined are presented in Table 1.

TABLE 1

Source	I	II	III	IV	V	VI
Antigua, Stebbing 1894	6 or 7	←——— 8–10 ———→				8
,, syntypes (B.M. 1928.12.1.2988–2993) new preparation .	6·6	9·9	8·9	10·9	9·10	9·8
Tortugas (B.M. 1952.6.10.2)	6·6	10·10	10·10	10·10	11·10	10·11
Cape Verde Is. (B.M. 79–10)	⎧6·7	9·9	9·9	9·9	9·9	9·10
Nilsson-Cantell (1927)	⎩6·8	9·9	9·10	9·9	9·10	–·10
Cape Verde Is. new preparation . . .	6·7	11·10	7+·10	8·10	9·10	12·11
,, ,, Calypso Exped. 1959 (Stubbings 1964*a*) . . .	6·7	11·10	11·11	12·12	12·12	10·11
Tema, Ghana, D. T. Gauld 2.9.59 . . .	6·6	9·9	7+·9	8·10	8·9	9·10

TABLE 1. Number of segments in the rami of the six cirri in specimens of *O. hoeki* from various sources.

The individual segments are less than twice as long as broad (Text-figs. 2*d*, 4*d*), sometimes longer by as little as a fifth only. The ratio of length to breadth of segments from cirri of a number of specimens of *O. hoeki* are given in Table 2, together with similar figures for *O. antiguae* :

TABLE 2

Species and source	No. of pairs of setae per segment		L/Br.
O. hoeki			
B.M. 1928.12.1.2988–2993 syntypes (Text-fig. 2*d*) .	4		1·50
B.M. 1952.6.10.2 Tortugas.	4		1·83
B.M. 79–10 Cape Verde	4		1·58
Calypso Cape Verde	3		1·21
Tema, Ghana (Text-fig. 4*d*)	3		1·41
		$\overline{m}$ = 1·51	
O. antiguae			
D. antiguae syntype (Text-fig. 6*f*)	6		3·0
B.M. 1952.2.14.1 Georgetown (Fig. 7*c*)	8		3·22
B.M. 1951.7.2.6 ,, ...	6		2·15
		$\overline{m}$ = 2·79	

TABLE 2. Number of pairs of setae on segments of the posterior cirri and length/breadth ratio in these segments in *O. hoeki* and *O. antiguae*.

The number of pairs of setae on each segment of the posterior cirri is three or four.

The caudal appendage is variable in length and in the length of its setae. It may not reach to the distal end of segment 1 of the protopodite of cirrus VI, as in a Tortugas specimen or may extend some way along the second segment as in the syntype (Text-fig. 2*e*), the Tema specimen (Text-fig. 4*e*) and a Cape Verde specimen (B.M. 79–10). The setae may reach to the distal end of segment 1 of the rami of cirrus VI (syntype) or scarcely to the base of that segment (Tortugas specimen). Stebbing was probably right in adducing this as a point of distinction from his *D. antiguae* as in the latter the setae do seem to be consistently longer (see Text-figs. 5*g*, 7*d*) but the character is not constant in *O. hoeki.*

The penis is of moderate length and tapers to a rounded tip. It is sparsely covered with soft hairlike setae arranged in rather diffuse rows. The tip bears a

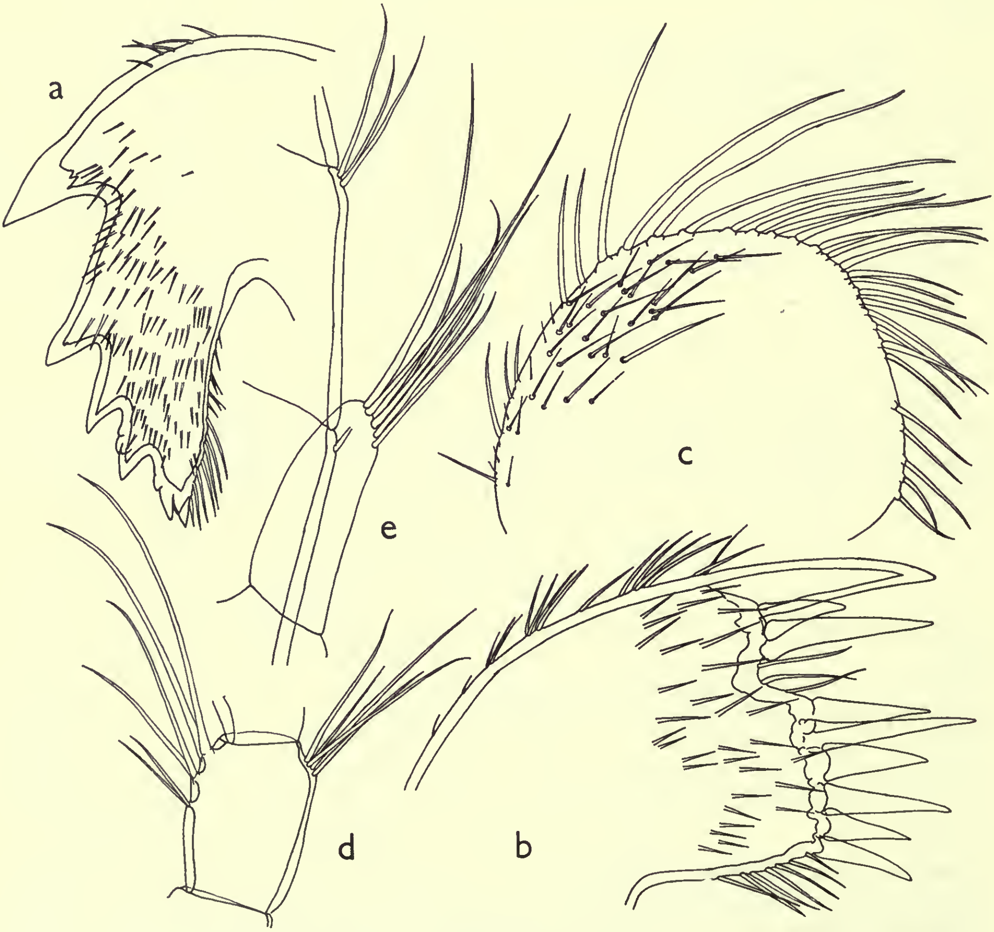


FIG. 4. *Octolasmis hoeki* (Stebbing) : appendages of a specimen from Tema, Ghana ; *a,* mandible ; *b,* maxilla I (both ×300) ; *c,* maxilla II ; *d,* segment 6 of anterior ramus of cirrus VI ; *e,* base of cirrus VI and caudal appendage (all ×183).

terminal tuft of rather stouter and longer soft setae. There is no terminal languet as in, for example, *O. lowei*. In several specimens examined, from different localities, the penis was of uniform width tapering toward the distal extremity. There was no widening of the middle portion as noted by Stebbing. This presumed character in two of Stebbing's specimens may be regarded as fortuitous and due to the state of contraction when preserved.

Octolasmis antiguae (Stebbing)

Dichelaspis antiguae Stebbing 1895, 19–20, pl. 2, figs. E–G.

MATERIALS EXAMINED : *Dichelaspis antiguae* Stebbing syntype, from Antigua, W.I. (B.M. 1928.12.1.2985–2987); *D. antiguae*, from Georgetown, Br. Guiana, (B.M. 1951.7.2.6); *D. antiguae* from Georgetown, Br. Guiana, (B.M. 1952.2.14.1).

Not known from the West African Cirriped fauna.

Stebbing (1895) separated *D. antiguae* from *D. hoeki* on the basis of the larger proportion of the capitulum covered by the valves, the contraction instead of widening of the tergum below, the slight emargination of the base of the carina and several characters of the appendages. The cirri were said to be more elongate than in *D. hoeki* and to have from 12 to 14 segments in all except the first pair; the segments being more slender and elongate and with more numerous spines. The caudal appendages also were said to be larger and more slender with longer terminal setae.

Outline drawings of scutum and tergum of British Guiana specimens are shown in Text-fig. 5 (B.M. 1952.2.14.1) from which the shape of these valves at different ages is apparent. The downward prolongation of the tergum noted by Stebbing is well seen in these figures of specimens in which the capitulum was well covered by scutum and tergum. The scutal border of the tergum is much straighter than in *O. hoeki* and in consequence the hook-like occludent lobe to the valve seen in that species is absent or at the most poorly developed. Furthermore the scutal margin becomes straighter with age.

If specimens of similar size are compared, e.g., Text-figs. 3*a*, 5*c* or Text-figs. 3*c*, 5*f*, the difference in tergal form between the two species will be apparent. *O. antiguae* appears to be rather smaller than *O. hoeki*. The greatest capitular length found was 3·44 mm. for *O. hoeki* but only 2·79 mm. for *O. antiguae*.

The labrum (Text-fig. 6*a*, syntype) has a series of well-developed teeth. The palp is oval and tapers slightly (Text-fig. 6*b* syntype). The mandible (Text-figs. 6*c*, 7*a*) resembles that of *O. hoeki* closely but the fourth tooth and the lower angle have more strongly developed subsidiary cusps. The maxilla (Text-figs. 6*d*, 7*b*) also resembles that of *O. hoeki*. The lower part of the biting edge is almost in line with that above the notch (Text-figs. 6*d* syntype and B.M. 1951.7.2.6) whereas in *O. hoeki* (Text-fig. 2*c*) the lower portion projects somewhat. This character again is not entirely reliable diagnostically as the lower angle may project in *O. antiguae* as shown in Text-fig. 7*b* (B.M. 1952.2.14.1). The second maxilla (Text-fig. 6*e*, syntype) is square and shows no distinguishing characters.

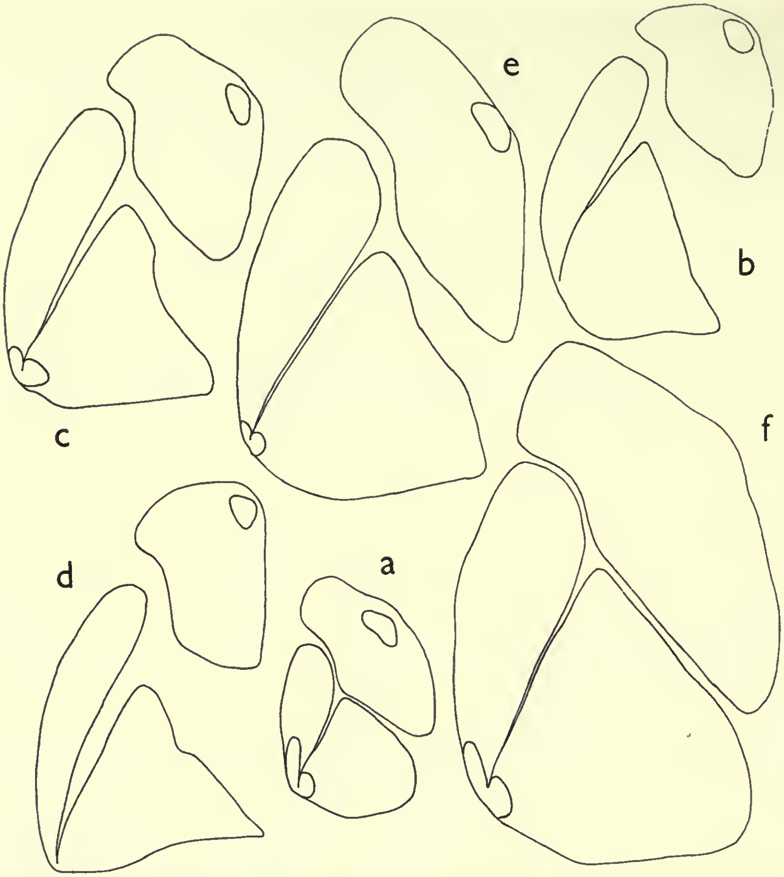


FIG. 5. *Octolasmis antiguae* (Stebbing) from Georgetown, British Guiana (B.M. 1952. 2.14.1): right scutum and tergum of specimens of increasing size showing greater coverage of capitulum and more elongated shape of tergum: for comparison with similar valves of *O. hoeki* shown in Fig. 3: capitular lengths *a*, 1·24 mm., *b*, 1·92 mm., *c*, 1·98 mm., *d*, 2·16 mm., *e*, 2·54 mm., *f*, 2·79 mm.

Re-examination of the cirri supports Stebbing's statement that they have more segments than do those of *O. hoeki*. The numbers found or recorded previously are shown in Table 3.

TABLE 3

	I	II	III	IV	V	VI
Stebbing 1895	7 or 8	←——— 12–14 ———→				
D. antiguae syntype	—	—	—	—	—	14·10
B.M. 1952.2.14.1 Georgetown	6·7	12·11	12·12	12·12	12·12	11·10
B.M. 1951.7.2.6 ,,	6·7	12·11	10·12	12·14	11·13	10+·13

TABLE 3. Number of segments in the cirri of four *O. antiguae* including Stebbing's original statement (1895) and those in a syntype.

The mean number of segments in cirri II–VI is nearly 12. As Table 2 shows the length/breadth ratio of individual segments is much greater than in *O. hoeki*, being more than 2 and often more than 3. The number of pairs of setae is consistently higher at 6–8 pairs per segment.

The single-jointed caudal appendage may extend to just beyond the distal end of the first segment of the pedicel of cirrus VI (Text-fig. 6*g*, 7*d*) or may be a little shorter. In this it does not differ clearly from the condition in *O. hoeki*. The terminal setae are appreciably longer as normally they extend to the distal end of segment 1 of the rami and often appreciably on to the second segment.

The penis is of moderate length, tapers towards the tip and has sparse hairs along its length and a terminal tuft of rather longer hair-like setae. It does not differ from that of *O. hoeki*.

It would appear, therefore, that the differences between *D. hoeki* and *D. antiguae* originally described by Stebbing (1895) and now re-examined are distinguishable. They are not so strongly marked that variability within the two species cannot bring

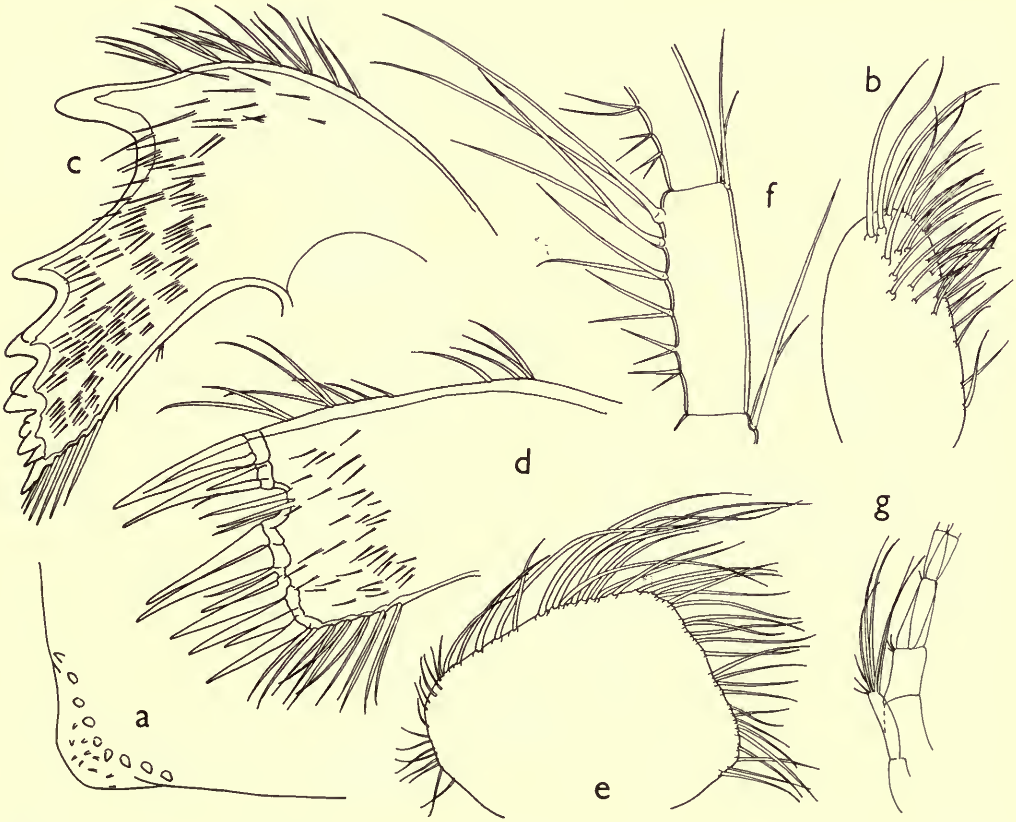


FIG. 6. *Octolasmis antiguae* (Stebbing): appendages of a syntype (B.M.): *a*, labrum; *b*, palp (both ×206); *c*, mandible (×294); *d*, maxilla I (×397); *e*, maxilla II; *f*, segment 7 of anterior ramus of cirrus VI (both ×206); *g*, lower part of cirrus VI and caudal appendage (×45).

about an overlap of individual characters. In consequence characters such as the shape of the tergum, the degree of dentation of the lower angle of the mandible, the straight or stepped edge of the maxilla and the length of the caudal appendage and its setae are individually unreliable as diagnostic characters. Taken collectively or when a series of specimens is available from the same source they afford a reasonably accurate guide to the species. The most reliable features are undoubtedly the proportions and setation of the cirral segments. In *O. hoeki* the length of the segments is less than twice the breadth and there are three or four pairs of setae. In *O. antiguae* the segments are more than twice, often over three times, as long as broad and there are from six to eight pairs of setae. These characters do not intergrade. Accordingly *Dichelaspis antiguae* Stebbing, 1895, is reinstated as a distinct species under the modern name *Octolasmis antiguae* (Stebbing, 1895).

The present investigation has shown that *O. hoeki* occurs on both sides of the tropical Atlantic whereas *O. antiguae* is known only from the much more restricted area of the Leeward Islands and British Guiana.

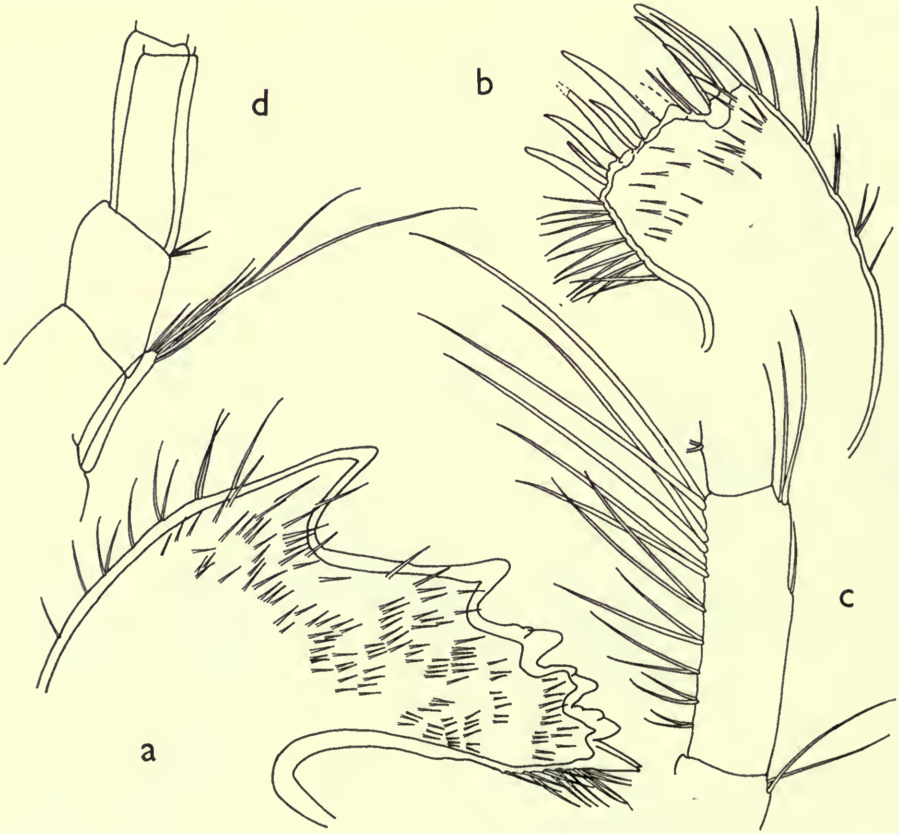


FIG. 7. *Octolasmis antiguae* (Stebbing): Appendages of a specimen from Georgetown, British Guiana (B.M. 1952.2.14.1): *a*, mandible; *b*, maxilla I; *c*, segment 7 of posterior ramus of cirrus VI (all ×300); *d*, lower part of cirrus VI and caudal appendages (×90).

VERRUCOMORPHA

VERRUCA

Verruca striata Gruvel

Taken by the "Talisman" south of the Cape Verde Islands, Lat. 16° 51′ N., Long. 27° 30′ W. in 598–633 m. (Gruvel, 1902*a*) this is the only species of *Verruca* so far recorded from tropical West African waters, though many species are known from the warm temperate waters of Madeira and the Azores. As yet, no species has been found in West African coastal waters.

BALANOMORPHA

CHTHAMALUS

Chthamalus stellatus (Poli)

Four varietal forms of *C. stellatus* are recorded in the literature from West Africa, vars. *stellatus*, *depressus*, *fragilis* and *bisinuatus*, in addition to records where no varieties are specified. The records of *fragilis* and *bisinuatus* are considered below, the former as *C. fragilis*. Records of "*depressus*" refer to *C. aestuarii* Stubbings. Of the remaining records of "*C. stellatus*" and "*C. stellatus* var. *stellatus*" it is highly improbable that all refer to the var. *stellatus*.

C. stellatus var. ***stellatus*** (Poli)

Locality: Ghana, Winneba: shore Section, ¼ m.^{2}, no. 1A, 4.3.50 (1 spec.).

The southward extent of var. *stellatus* is difficult to determine from records owing to the confusion of forms in earlier reports. Records in the literature up to 1943 were cited in Stubbings (1961*a*). The more northerly records, namely Morocco (Broch, 1927), Rio de Oro (Nilsson-Cantell, 1939*b*), Mauretania (Broch, 1924*b*) and Madeira and Cape Verde Is. (Darwin, 1854) are acceptable. The Cape Verde record is confirmed by "Calypso" material (Stubbings, 1964*a*). Sourie (1954) records only *C. stellatus* in his study of the ecology of rocky shores from Mauretania to Guinea, thus including Senegal. Yet there were no *C. stellatus* in the cirripede collections from I.F.A.N., Dakar, studied by the writer, only two samples of *C. dentatus*. Assuming Sourie's identifications to be correct, some at least of which were made by Professor Hj. Broch of Oslo, this implies an abrupt change of predominant species in the region of Cape Verde. The northern species *C. stellatus* is predominant in Mauretania and south of the Cape the tropical and southern hemisphere species *C. dentatus*. Records from further south are suspect because of the possibility of confusion with *C. aestuarii* and *C. dentatus*. Thus Gruvel (1912) records *C. stellatus* from Libreville (Gabon) and Kitombe, Banana, at the mouth of the Congo. Weltner (1897) gives Victoria, Cameroons and Kolosvary (1943*a*) Fernando Po, as localities. There are no *C. stellatus* in the extensive collections from the Congo estuary, including Kitombe, in the collections of the Musée Royal de l'Afrique Centrale, Tervuren

(Stubbings, 1964*b*). Whilst " Calypso " did not visit Fernando Po, collections were made at the other islands in the Gulf of Guinea and no *C. stellatus* were collected (Stubbings, 1961*b*). In both areas *C. dentatus* was collected, and *C. aestuarii* is common in the Congo estuary. Weltner's record from Victoria is presumably correct as specimens were taken there by " Atlantide " (Stubbings, 1961*a*).

It would seem, therefore, that in West Africa *C. stellatus stellatus* is only common on the north-west coast (Morocco, Mauretania) and in Madeira and the Cape Verde Islands. It may occur sporadically in small numbers further south, certainly as far as the Cameroons, but in general it is replaced south of Cape Verde by *C. dentatus* in more exposed conditions and by *C. aestuarii* in the more sheltered conditions of estuaries.

C. stellatus var. ***bisinuatus*** Pilsbry

C. stellatus var. *bisinuatus:* Stubbings, 1961*a*, 18–19, text-fig. 3.

Specimens from Lagos, Nigeria in the University Zoological Museum, Copenhagen (Stubbings, 1961*a*) belong to this variety. There are no other West African records of this otherwise Brazilian variety.

Chthamalus dentatus Krauss

LOCALITIES: Gambia: No. 3 Gambia Lightship, 22.9.48, pres. M. W. H. Bishop, B.M. 1950.7.19.1 (several spec.).

Sierra Leone: Kissy, Sierra Leone River, on rocks above littoral fringe, coll. A. R. Longhurst, B.M. 1956.1.7.4 (32 spec.).

Ghana: (1) Ada, on launch " Akuse " (21 spec.); (2–9) Accra, (2) Christiansborg shore, 15.1.49 (several young uneroded spec.); (3) on *Thais haemastoma* L., 14.2.49 (several hundred spec.); (4) from splash zone, 14.2.49 (110 + 22 juv. + 5 dead spec.); (5) on *T. haemastoma*, *T. nodosa* L. and *Patella safiana* Lam., 17.3.49 (c. 100 + 50 juv. + 29 dead spec.); (6) on a limpet, 5.11.49 (123 + 20 juv. + 45 dead spec.); (7) on a large *B. t. tintinnabulum*, 19.11.49 (few spec.); (8) on a rubber tyre fender, 14.3.51 (several hundred spec.); (9) HWM on sandstone rock, 19.3.58, coll. H.G.S. (91 + 45 juv. spec.); (10–12) Winneba: (10) on rock and shells including *T. haemastoma*, *P. safiana* and *Mytilus perna* L., 15.11.49 (453 + 264 juv. + 32 dead spec.); (11) on similar substrate, 22.11.49 (several hundred spec.); (12) shore section made on 3/4.3.50 (over 1500 spec.); (13–16) Apam; (13) " high on shore ", 16.2.49 (many spec.); (14) on *Gadinia afra* Gmelin (44 + 25 juv. spec.); (15) embedded in a sponge (1 spec.); (16) on Gastropods including *T. haemastoma*, *T. nodosa* and *Nerita senegalensis* Gmelin (several hundred spec., about half juv.); (17) Sekondi, High Land Plateau, on sandstone rock, 21.2.49 (numerous spec.); (18) Prince's Town shore, 15.4.49 (1 spec.); (19) Axim, Hospital reef, H.W.M., 13.4.49 (several hundred spec.); (20) Axim, on reef, *B. t. tintinnabulum* and a limpet *Fissurella nubecula* L., 17.1.51 (184 spec.); (21) Ankobra ferry, on log, 19.2.49 (many spec.); (22) Half Assini, on wreck, —2.49 (217 + 2 juv. + 7 dead spec.); (23) Prampram, on rock fragment, —.11.37, pres. Miss V. J. Foote, B.M. 1952.5.7.2 (numerous spec.).

Nigeria: (1) Bonny River, fairway buoy in river mouth, in splash zone and down to 1 ft. below float line, with *B. pallidus* (45 spec.); (2) Bonny, on New Pier on concrete at HW and above with *C. aestuarii*, 28.11.57 (4 spec.) (H.G.S. 331).

I have seen further material from Labadi Beach, Accra, and Tema, Ghana, the west mole, Lagos and from Victoria, Cameroons, all collected by Dr. Eyvor Sandison.

This extensive material includes young and old, uneroded and eroded specimens, single individuals and densely packed colonies, the last sometimes showing some shell elongation. Where erosion is heavy shells become low and featureless and when densely packed sutures and even boundaries between specimens become indistinguishable. Young uneroded specimens are fawn or pale-brown with a thin epidermis.

The compartments are practically smooth, with only feeble longitudinal furrows on some of them. Growth lines are visible intermittently. The sutures are rather irregularly sinuous externally and not dentate.

With erosion the worn areas become marbled fawn or brown and white with the brown epidermis restricted to the newer basal parts of the compartments. In more heavily eroded specimens the shells may be wholly white.

The Nigerian specimens from a buoy at Bonny are large isolated broadly conical individuals, the largest 12 × 9·5 mm. diameter × 5 mm. high. In most the lower part of the paries is " narrowly and regularly folded " as described by Darwin (1854: 463) for shipborne specimens.

The development of the characteristic dentate sutures is variable. When well-

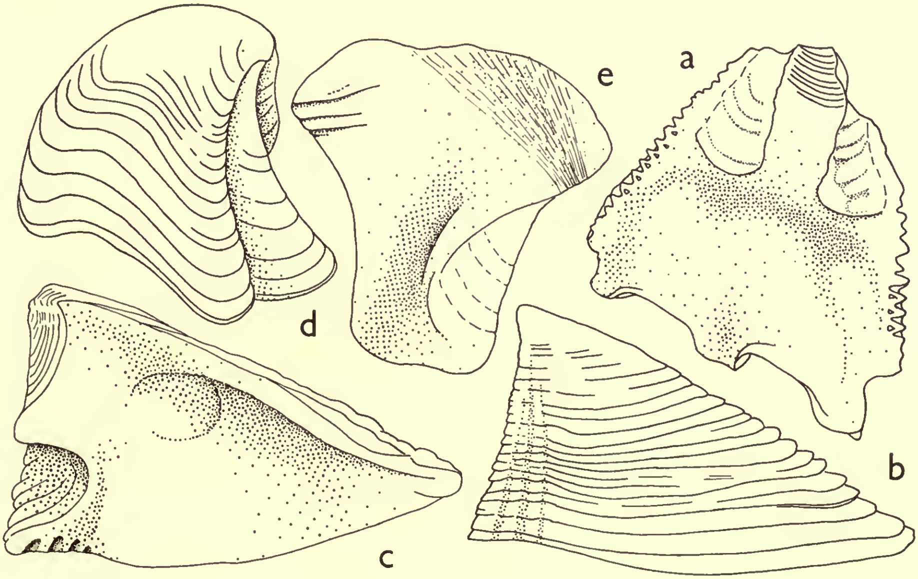


FIG. 8. *Chthamalus dentatus* Krauss: specimen from rubber tyre fender at Accra. *a*, internal view of rostro-lateral compartment with well-developed dentate sutures (×14); *b*, *c*, external and internal views of the scuta and *d*, *e*, of the terga of the same individual (all ×23).

formed and uneroded the zigzag sutures are clearly visible externally. The sutural surfaces or " teeth " are short ridges with sharp, angular crests, the sutures then appearing sharply dentate, or with smoothly rounded crests in which case the sutures become sinuous. The broader and lower these ridges the more the sutural line departs from a zigzag and approaches a straight line. Both angular and rounded sutural teeth are seen in the left rostrolateral compartment in Text-fig. 8*a*. In eroded shells it is often impossible to discern the dentate margin to the compartments. They can then be seen only from the inside of the shell or after dissociation of the compartments. The dentations may be obliterated by distortion during the growth of close-packed low-growing specimens. In elongated specimens the teeth may be very small or obscure on the lower part of the sutures which become more or less sinuous in outline.

Internally the dentations are often in a narrow groove which renders them less visible. In close-packed specimens the groove may be almost closed in the lower part and the sutures show only 1 or 2 dentations in the older part. These were presumably produced before the barnacles became contiguous. The clearest dentations are shown on specimens grown singly in sheltered places free from erosion, such as on piers or buoys.

Two forms of the shell and an internal view of the tergum were shown by Darwin (1854, pl. 18, figs. 3*a–c*). No figure of the scutum has been published. Internal and external views of both opercular valves are given here. The scutum (Text-fig. 8*b*, *c*) agrees well with Darwin's description in the very prominent articular ridge, which is most protuberant about the middle of the articular border and in the deep adductor pit and the row of small pits for the depresser muscles referred to by Darwin as " distinct, though minute, pits . . ." (1854 : 464). In some young specimens the broadest part of the articular ridge may be nearer the apex when the valve comes to resemble that figured by Pilsbry (1916, fig. 83) as *C. fragilis* Darwin. Specimens with this type of scutum but with well developed dentate sutures are in the collection so these are presumably *C. dentatus* though somewhat divergent from the norm. Externally uneroded scuta bear fairly prominent regular growth lines.

The tergum (Text-fig. 8*d*, *e*) agrees with Darwin's figure in the strong articular ridge and strongly curved carinal margin. The depressor muscle crests are on a projecting portion—" Auf einer vorspringenden Partie "—as remarked by Nilsson-Cantell (1921 : 284).

Mouth parts have been figured previously by Nilsson-Cantell (1921). There is a long series of small teeth and a row of hairs on the labrum (Text-fig. 9*a*). In some Nigerian specimens the labral teeth are less developed and less numerous. The palp (Text-fig. 9*b*) is broadly oval with the inner margin straight or slightly concave. The mandible (Text-fig. 9*c*) is close to that shown by Nilsson-Cantell (1921, fig. 52*c*, *d*). There have been divergent reports on the condition of the lower angle. Darwin (464) described it as " coarsely pectinated " but Nilsson-Cantell found most specimens to have only fine bristles here, a view concurred in by Barnard (1924). However, Nilsson-Cantell (1921) found an individual in which spines occurred among the hairs on the lower angle (his fig. 52*d*). The specimen here figured has fine spines on the lower angle.

Maxilla I (Text-fig. 9*d*) has a broad notch with small spines. Below it, the median spines are but little larger than the lower ones into which they grade smoothly. Maxilla II (Text-fig. 9*e*) is broad with a deeply concave anterior margin, the median concavity being devoid of bristles as noted by Nilsson-Cantell.

The number of segments in the cirri of two specimens, presumably from Madagascar, were given by Nilsson-Cantell (1921). These compare favourably with counts

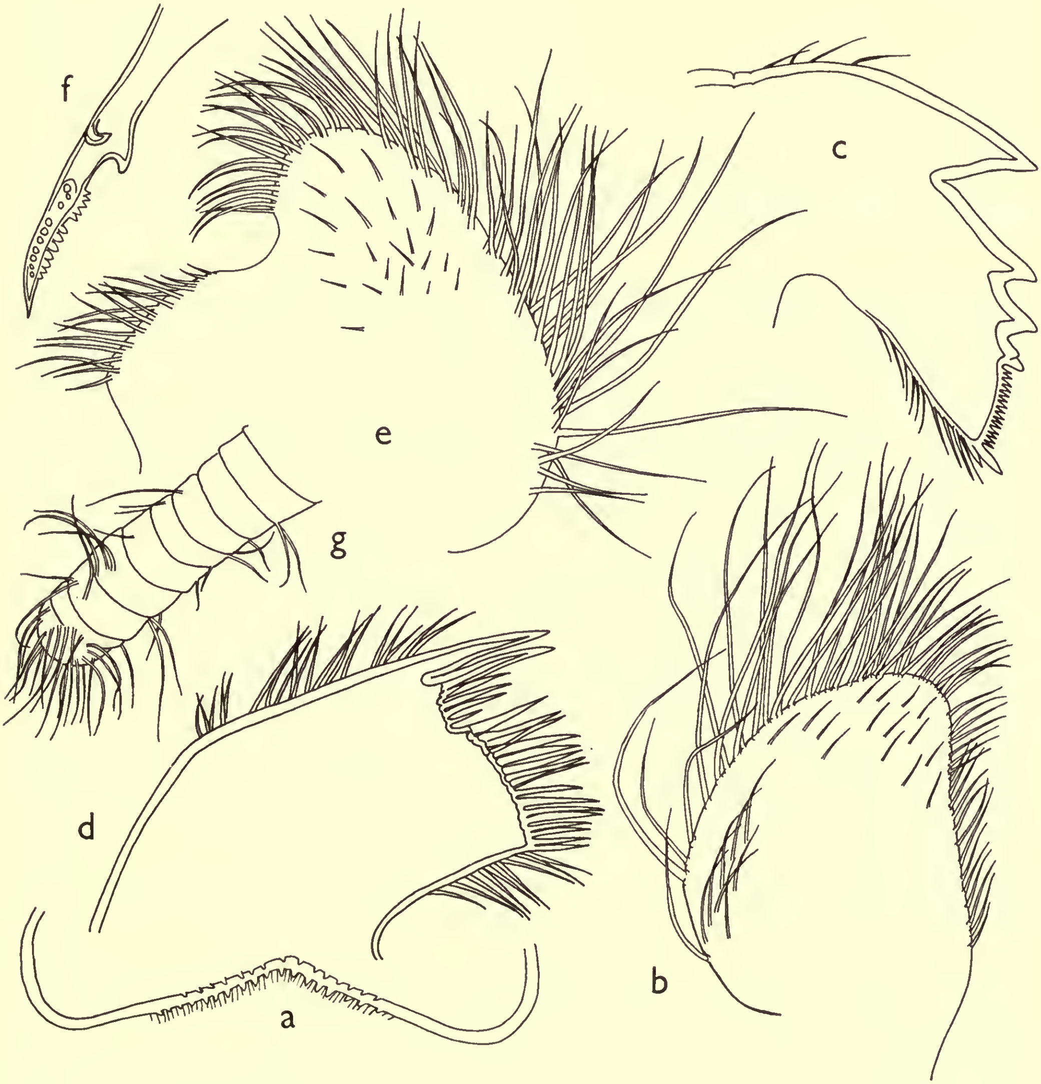


FIG. 9. *Chthamalus dentatus* Krauss : *a*, labrum ; *b*, palp ; *c*, mandible ; *d*, maxilla I ; *e*, maxilla II (all ×170) of a specimen from rubber tyre fender, Accra : *f*, compound spine from tip of cirrus II (×350) of a specimen from a buoy at Bonny, Nigeria ; *g*, tip of penis (×80).

made on specimens from Christiansborg, Accra and from Nigeria collected by the author. The number of segments in the right and left cirri of two specimens from each locality are given in Table 4.

TABLE 4

Specimen		I	II	III	IV	V	VI	Scutum mm.
Accra	L	7·6	6·5	15·15	16·16	18·18	18·19	1·85
	R	7·6	6·5	14·15	15·17	18·17	19·18	
Accra	L	7·8	7·5	14·14	17·16	16·16	18·18	2·11
	R	8·7	7·6	13·12	15·17	18·18	19·18	
Nigeria	L	8·7	7·7	20·19	23·23	24·24	24·24	3·51
	R	9·7	7·6	20·21	23·24	24·24	25·24	
Nigeria	L	7·6	6·5	18·19	22·23	24·25	27·24	3·44
	R	7·6	6·5	17·18	22·23	25·24	25·25	

TABLE 4. Number of segments in left and right cirri of four *C. dentatus*, with scutal lengths as an index of barnacle size.

The number of segments in the longer cirri in the Nigerian specimens but not in those from Accra is thus rather higher than previously recorded. Because of the distortion of some of the shells due to crowding the relative size of the above specimens is indicated by reference to the length of the base of the scutum. The Nigerian specimens were considerably larger than those from Accra, probably attributable to a more favourable environment on the navigation buoys. This size variation could account for the observed difference in segment counts. Pectinate spines (Text-fig. 9*f*) are present on the terminal segments of cirrus II.

The penis is closely annulated, the annuli broadening towards the distal end until about half as long as broad (Text-fig. 9*g*). The distal segments are sparsely clothed with long hair-like setae. A ring of similar setae surrounds the tip.

C. dentatus is found on the whole west coast of Africa, south of Cape Verde. There seems little doubt of its northern limit. There are few specimens in the IFAN collections at Dakar, suggesting that it is not common there. Furthermore, Sourie (1954) who investigated the coastline of Mauretania and Senegal rather thoroughly does not record it at all. Hoek (1883) records *C. dentatus* from the Cape Verde Is., but from his account the identification is uncertain. The species was not found in the archipelago by the " Calypso " expedition in 1959.

In the Gulf of Guinea the species is known from the islands of Principe and São Tomé (Stubbings, 1961*b*). South of the River Congo there are few records, largely due to the lack of collecting on this coastline. At the Cape it is common from False Bay to Durban (Sandison, 1954). According to Miss Sandison it is uncommon in the cold water current on the west side of the Cape Peninsula and this, presumably, will apply to the Atlantic coast of South Africa and South-West Africa where influenced by the cold Benguela current. As at Capetown, however, it is not entirely absent from this section of the coast, as witness the record for Walvis Bay (Stubbings, 1963).

Four isolated records, two in Madagascar (Nilsson-Cantell, 1921), one each in Mauritius (Weltner, 1897) and Aden (cited by Nilsson-Cantell, 1921, without authority) extend the distribution of *C. dentatus* into the Indian Ocean and a fifth (Weltner, 1897) to Singapore.

Chthamalus aestuarii Stubbings

Chthamalus aestuarii Stubbings, 1963, 7, text-figs. 2, 3.
Chthamalus stellatus depressus: Nilsson-Cantell, 1938*b*, 177, text-fig. 2.
Chthamalus cirratus: Kolosvary, 1941*b*, 70.
Chthamalus cirratus: Kolosvary, 1943*a*, 75.
Chthamalus stellatus f. *depressus:* Gauld, 1957, 10.
Chthamalus rhizophorae: Longhurst, 1958, 32, 59, 85.
Chthamalus withersi: Longhurst, 1958, 59, 85.

LOCALITIES : Sierra Leone : (1) Bunce I. Sierra Leone River, on mangrove, 1955, coll. A. R. Longhurst, B.M. 1956.1.7.3 (as *C. rhizophorae* Oliveira); (2) Sierra Leone River on mangrove, July 1955, coll. A. R. Longhurst B.M. 1957.6.3.3 (as *C. withersi* Pilsbry); (3) Reef at Wellington, Sierra Leone River on mangrove, 19.7.55, coll. A. R. Longhurst, B.M. 1956.7.1.5 (as *C. withersi*).

Ghana: (1) R. Densu on mangrove, 3.4.49.; (2) Prince's Town, on mollusc shell fragment, 15.4.49 (1 spec.); (3) Ada, R. Volta, at H.W.M. on pier, 15.3.49 (numerous spec.).

Nigeria: (1) Port Harcourt on concrete " dolphin ", 19.12.57 (37 spec.) (H.G.S. 350); (2) Bonny R. estuary, on concrete pier at Bonny, 28.11.57 (6 spec.) (H.G.S. 323); (3) Opobo, Imo River, E. Nigeria, on pier and on *B. pallidus*, 11.1.58 (12 spec.) (H.G.S. 373).

In addition I have seen specimens collected by Miss Sandison from Badagri Creek and Kuramo Creek, near Lagos, from Porto Novo lagoon, Dahomey and the R. Baka, near Elmina, Ghana, all on bark, probably of mangroves.

This species was described fully from material from the Congo estuary by Stubbings (1963). The present material establishes its presence over the whole tropical West African coastline where conditions are favourable.

In examining further material from a greater geographical area some variations in form have been observed and are illustrated here. In my original illustration a slightly eroded specimen in which growth lines were not apparent was figured. This specimen had radiating dark brown or black lines on the parieties. The young and uneroded specimen now figured (Text-fig. 10*a*) from the Sierra Leone river lacks these black lines and the incremental lines are quite distinct. The scutum (Text-fig. 10*b,c*) has a much more oblique basi-tergal angle and the basal margin is less strongly bowed. In other respects the scutum resembles my earlier figures, in particular in the protuberant apical region of the articular ridge.

Internally the tergum shows some variation. The articular furrow is always well developed and rather broad. Text-figs. 10*d, e* are external and internal views of the terga of the specimen from which the scuta came. The articular furrow here was of average size. The depressor muscle crests on the other hand were reduced to one, instead of the normal three or four as in Text-fig. 10*f*. This latter specimen had a very broad open articular furrow with a rather uneven surface. A specimen from Port Harcourt (Text-fig. 10*g*), showed a similar rough broad articular furrow. This

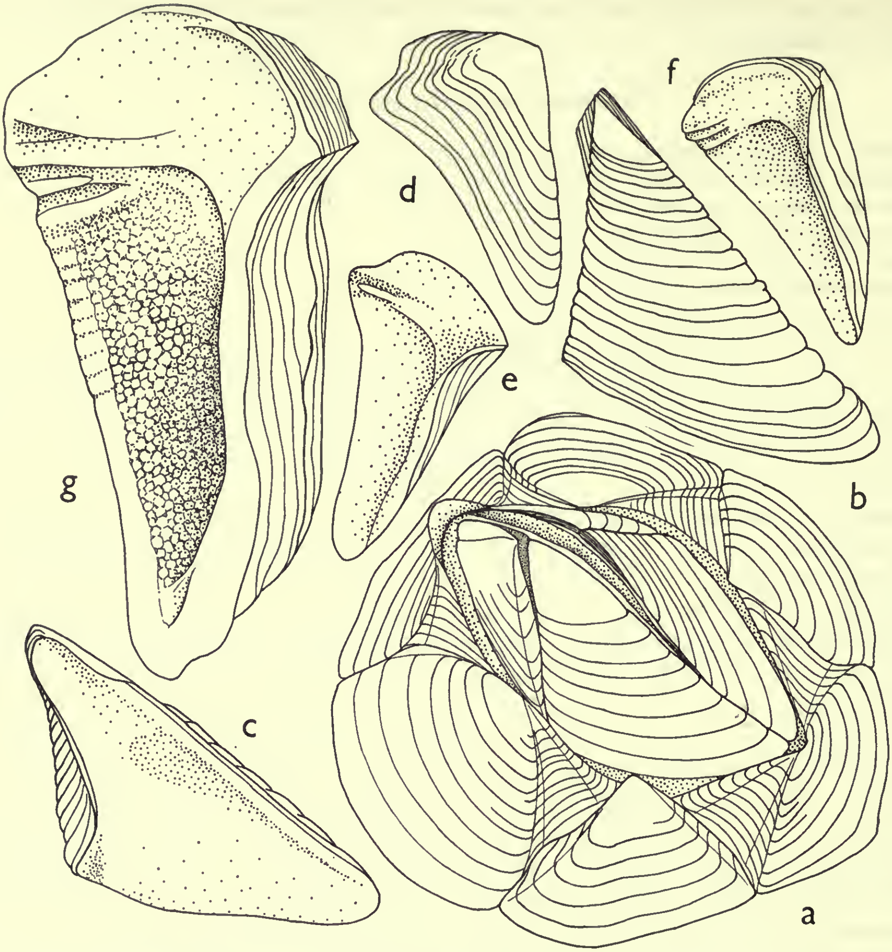


FIG. 10. *Chthamalus aestuarii* Stubbings: *a*, uneroded specimen from Sierra Leone River showing distinct growth lines and no pigment bands (×17); *b*, *c*, external and internal views of the scuta, and *d*, *e*, of the terga of another Sierra Leone specimen; *f*, internal view of tergum of a third specimen (*b–f*, all ×65) (B.M. 1957.6.3.3); *g*, tergum of a specimen from Port Harcourt, Nigeria, with broad articular furrow and roughened internal surface (×28).

rather massive valve was noteworthy for the very rough interior and for the apparent differentiation of a tiny spur from the basi-scutal angle.

The mouth appendages with the exception of Maxilla II were illustrated by Stubbings (1963). Minor variations are shown by the appendages illustrated in Text-fig. 11. In a Port Harcourt specimen (Text-fig. 11*a*) the row of teeth on the labrum is rather shorter. In a specimen from Sierra Leone (B.M. 1957.6.3.3) (Text-fig. 11*b–d*) the mandible has 3 simple teeth without subsidiary cusps. In the maxilla the central group of spines is demarcated by a very weak notch below as well as by one above. In this it approaches *C. rhizophorae* Oliveira but the frontal margin of the maxilla is still straight and not stepped as in *C. rhizophorae*. Maxilla II has a concave anterior margin and a very strongly convex posterior margin. The setae are all simple. The cirri are as previously described. The number of segments in the right and left cirri of a Sierra Leone specimen are given in Table 5.

TABLE 5

	I	II	III	IV	V	VI
right	8·6	8·8	17·20	25·?*	24·?*	20·23
left	8·6	9·9	24·24	19·22	21*+·24	21*+·21*+

* cirri IV and V of the right side lacked one ramus : cirri V and VI of the left side lacked the last few segments.

TABLE 5. Number of segments in right and left cirri of a specimen of *C. aestuarii*.

These figures are in good agreement with the segmentation of the cirri of a Congo specimen (Stubbings, 1963 : 9).

The above-sited synonymy was reviewed at some length by Stubbings (1963) and that discussion need not be repeated here. With the exception of *C. withersi* and *C. rhizophorae* the species confounded with *C. aestuarii* have in general been described and figured adequately in the past. The appearance of full-grown *C. withersi* is now revealed through the work of Pope (1965) but no further figures of *C. rhizophorae* have appeared since the original descriptions by Oliveira (1940, 1941).

As Miss Pope has cast doubt on the status of *C. rhizophorae* as a separate species—and by implication of *C. aestuarii* (1965 : 40) a further series of figures of scuta and terga of *C. rhizophorae* from the same general area as the type are given here (Text-fig. 12).

Comparison of these valves with those of *C. aestuarii* (Text-fig. 10 and Stubbings, 1963, fig. 2) shows at once the differences and resemblances in the opercular valves of the two species. The shape of the articular ridge of the scutum alone (Text-figs. 10*b*, *c* and 12*a*, *c*) separates the two species immediately. The presence of pits in the inner surface of the scutum and to a lesser extent of the tergum also seems characteristic of *C. rhizophorae*. These pits are visible in Oliveira's (1940) photographs, but were not indicated in his line drawings of the valves (1941). Very heavy and thick valves may occur in *C. rhizophorae* (Text-fig. 12*c*, *d*) and in terga of this type the articular surface is even broader than in *C. aestuarii*.

The three 'species' have been compared using material from Queensland (*C. withersi*), Brazil (*C. rhizophorae*) and West Africa. The chief points distinguishing *C. aestuarii* from *C. withersi* are described below.

The psi (*ψ*) shaped articulation of the opercular valves is shown by all except young uneroded *aestuarii* but not by *withersi*. The articular ridge and furrow of the scutum form only " a shallow wavy fold and trough " (Pope, 1965 : 42) in *withersi*. There are scarcely any interlocking surfaces. It is, in fact, one of the most poorly developed examples of this structure in *Chthamalus*. In *aestuarii* the ridge is much stronger and interlocks with the tergum. The area of the ridge towards the valve apex projects beyond the tergal margin of the scutum. In the tergum the chief

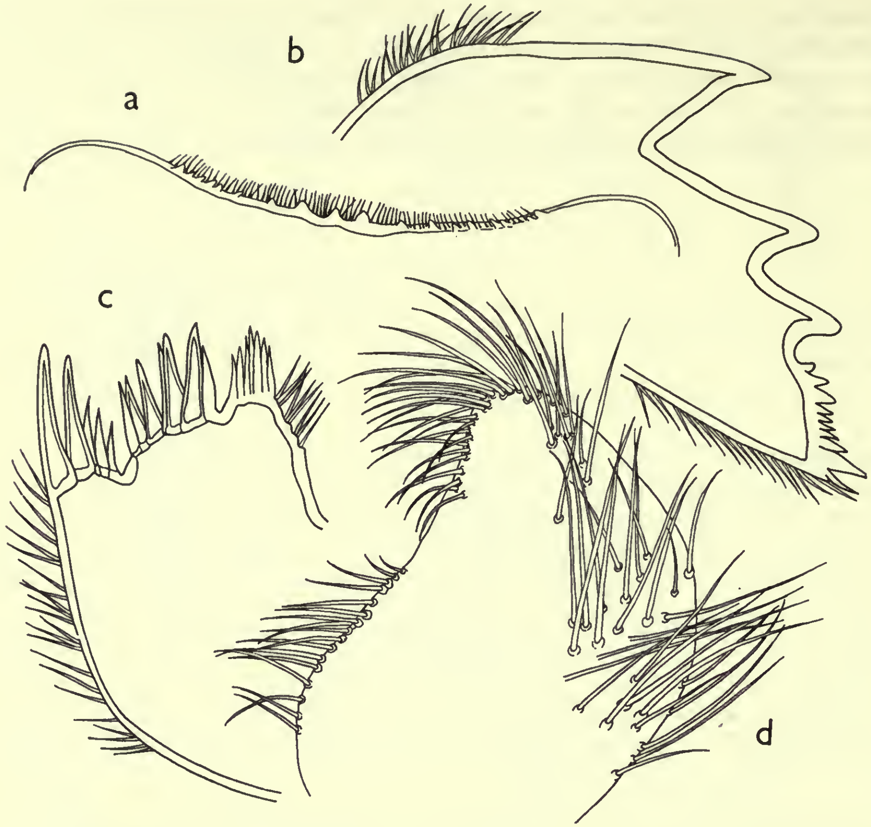


FIG. 11. *Chthamalus aestuarii* Stubbings: *a*, labrum of a specimen from Port Harcourt; *b*, mandible, *c*, maxilla I, *d*, maxilla II of the same Sierra Leone specimen as the opercular valves in Fig. 10*b–e* (all ×170).

difference lies in the articular margin. As in *withersi* it is inturned at right angles to the plane of the main valve surface. But whereas in *withersi* there is only a very narrow articular surface in *aestuarii* it is much broader. To accommodate this greater articular surface the scutal margin is turned further back on itself so that much of the articular surface lies in a plane parallel to that of the main part of the valve.

In young *rhizophorae* the articular ridge of the scutum is only modestly developed but its middle portion projects forward over the articular groove. In old and massive valves which have only suffered slight erosion, the interlocking surfaces of scutum and tergum are very broad and flat, being again roughly parallel to the external surface of the valves.

On these characters it is quite possible to distinguish the three species.

Differences in the mouth appendages are rather variable. The redescription of the labrum by Miss Pope removes the earlier distinction of a short line of teeth on its edge in *withersi*. The *withersi* mandible evidently varies in the number of major teeth from three to occasionally four. The curiously " hard " outline of the teeth shown by Pilsbry and present in my material—seemingly due to the straight margins of the teeth in profile—is not seen in *aestuarii* or *rhizophorae*. The lower angle terminates in a few short spines in my *withersi* but in *aestuarii* and *rhizophorae* the number of spines is greater and they form a " comb " below the third tooth. There is some variability in these spines. Those shown in Text-fig. 11*b* are appreciably shorter than those in my original description (Stubbings, 1963, fig. 3*c*).

In *withersi*, and *rhizophorae* the edge of maxilla I has two notches and is " stepped ", the lower sections protruding well in front of that or those above. In *aestuarii* the edge is almost straight with a small notch below the upper group of spines. In the specimen originally figured there was no lower notch. In that now shown there is a slight indication of this lower notch. It is more apparent than real, its presence being emphasized by the disposition of the spines and the thickening of the cuticle here.

In view of the above differences it is considered that *C. aestuarii* and *C. withersi* are distinct species albeit occupying very similar habitats. Though less material has been available, it would seem that *C. rhizophorae* also is a distinct species.

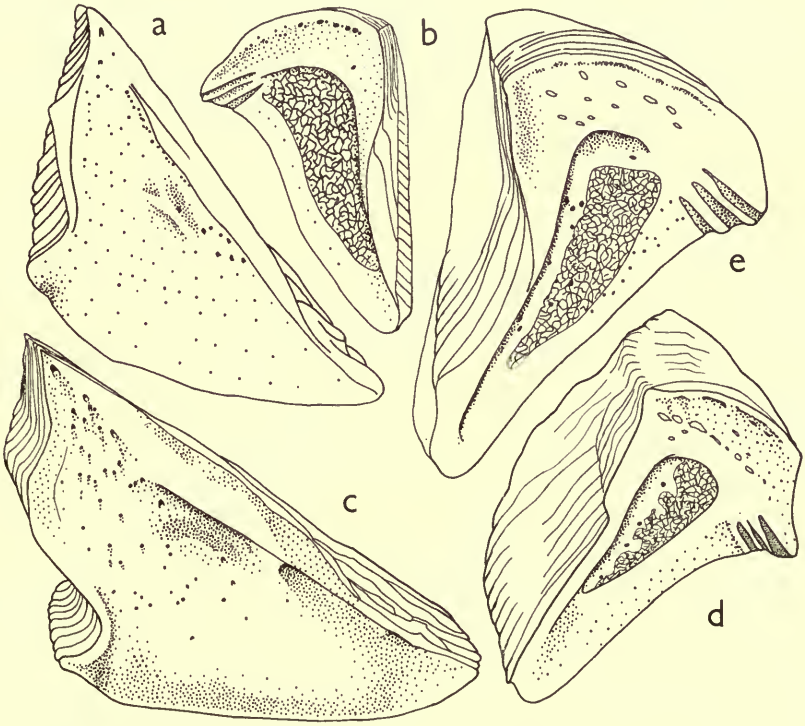


FIG. 12. *Chthamalus rhizophorae* Oliveira : internal views of *a*, *b*, right scutum and tergum of one specimen, *c*, *d*, right scutum and left tergum of a second, and *e*, left tergum of a third specimen (all ×12).

Chthamalus fragilis Darwin

LOCALITY: Bota, Cameroon: on *Ostrea* sp. from a lighter, 21.2.58 (22 spec.) (H.G.S.426).

Chthamalus fragilis was recorded by Broch (1927*a*) from Tangier and is grouped as an Atlantic–Mediterranean species by Kolosvary (1941*b*), presumably on this record. There are no other records for north or west African coasts. The species is common apparently on the warmer Atlantic coastline of North America and in the West Indies (Darwin, 1854; Pilsbry, 1916; Nilsson-Cantell, 1933, 1939*c*; Kolosvary, 1943*a*; Weiss, 1948). Broch (1927*a*) did not figure the Tangier specimens. Figures have been given of American (Pilsbry, 1916, pl. 70 and text-fig. 83) and West Indian specimens (Nilsson-Cantell, 1928, text-fig. 14; 1933, text-fig. 1). The walls of the present specimens are smooth and white with a thin pale yellow persistent epidermis. Growth lines are present and easily traced but are very low. Radii are present but small, and the interparietal areas are very narrow. The tergum (Text-fig. 13*a*) agrees closely with that figured by Pilsbry (1916, text-fig. 83A). The spur is distinct from the basi-scutal angle but is rounded, not pointed as in some of Pilsbry's examples and in the two shown by Nilsson-Cantell (1933, text-fig. 1). The scuta are shown by Pilsbry only. That figured here (Text-fig. 13*b*), is in good agreement with Pilsbry's text-fig. 83C and his pl. 70, fig. 3. The depressor muscle pit is not appreciably deeper than the shallow depression behind the articular ridge. The adductor pit lies in a very pronounced furrow parallel to the occludent margin of the valve.

The mouth parts are, as stated by Pilsbry, very like those of *C. stellatus stellatus* and agree with this author's figures for the latter species.

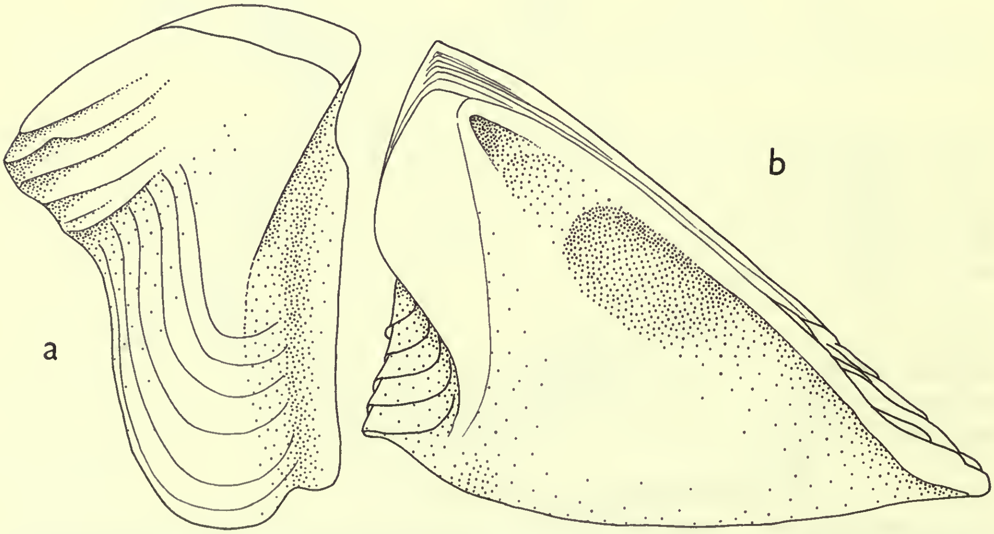


FIG. 13. *Chthamalus fragilis* Darwin: internal views of *a*, tergum and *b*, scutum of a specimen from Bota, Cameroon (×80).

Pachylasma giganteum (Philippi)

This Mediterranean species has been recorded twice only from other waters. Gruvel (1907*b*, 1910) records it from Simonstown, South Africa in the collections of the " Gauss " and Kolosvary (1943*a*) from Sette Cama, Gabon. The latter is the only record for West Africa. Darwin (1854) remarks that *P. giganteum* is often associated with *B. tulipiformis*, but although the latter species has been collected frequently no *Pachylasma* have been recorded.

Other species of *Pachylasma* have been described from the Indian Ocean, South-east Asia and Australia. Specimens of all species of *Pachylasma* are rare and the degree of variation within any one species is uncertain. As Nilsson-Cantell (1932*b*) has pointed out, it is probable that some at least of these described species are no more than sub-species of *P. giganteum*. Until more material is available especially of *P. giganteum* from the Mediterranean and Atlantic the validity of these species, and therefore, the geographical distribution of each, must remain problematical.

BALANUS

Balanus tintinnabulum (Linn.)

Only one variety or subspecies of *B. tintinnabulum* is common on the west coast of Africa, namely *B. tintinnabulum tintinnabulum* (L.). The occurrence of two other varieties has been fairly definitely established but the presence there of several others mentioned in the literature is highly doubtful.

Balanus tintinnabulum tintinnabulum (L.)

Balanus tintinnabulum tintinnabulum Pilsbry, 1916, 55–57, pl. 10, figs. 1–1*e*.

LOCALITIES: Gambia: (1) off Gunjur, on hull of shark fishing boat, 3.3.51, coll. M. H. Routh, B.M. 1952.10.2.3 (14 half grown and 11 very small spec. <11 wks. old); (2) from sea water intake of " African Queen ", encrusted with *B. pallidus* and a few *B. amphitrite amphitrite* and *B. trigonus*, 2.10.51 coll. M. H. Routh, B.M. 1952.10.2.5 (3 part-grown spec.).

Sierra Leone: (1) hull of S/T " Cape St. Mary ", 2–3 m., –.12.54 coll. A. R. Longhurst, B.M. 1956.1.7.10 (3 fairly large + 1 small spec. and remains of another); (2) Sierra Leone River, probably from ship's hull, –.7.55 coll. A. R. Longhurst, B.M. 1957.6.3.4. (5 small spec.).

Ghana: (1) Accra Sta. 86 (several clusters of small dead spec.); (2) Prince's Town, on a fragment of a large mollusc shell bored by *Kochlorine hamata* Noll (Cirripedia Acrothoracica) and by the Lamellibranch *Lithophaga aristata* (Solander) Dillwyn (2 dead spec.); (3) Half Assini, from a wreck, with epizoic *C. dentatus* (1 half-grown spec.); (4) Hospital Reef, Axim, including 3 small dead specimens overgrown by sponge, several clusters of mixed sizes, 2 damaged specimens and a shell with encrusting algae and *C. dentatus* (numerous spec.); (5) Apam shore, including two small, thin and fragile specimens on a siliceous sponge and three large ones overgrown by Zoanthid colonies (8 spec.); (6–7) Winneba: (6) shore, encrusted with calcareous algae and with attached *C. dentatus* and *Mytilus perna* L. (3 spec.); (7) rock face, with attached *C. dentatus*, encrusting algae and Polyzoa (2 large spec.); (8–19) Accra; (8) on moorings (1 small spec.); (9) boat buoy, attached to *C. dentatus* and associated with *B. amphitrite* (1 small spec.); (10) on copper sheathing of boat and attached to *B. amphitrite amphitrite* (3 juv. spec.); (11) Christiansborg shore, embedded in a sponge but attached to the hard substrate (1 spec.); (12) the same, 15.1.49 with a few small epizoic *C. dentatus* (2 spec.); (13) the same, part attached to the keyhole limpet *Fissurella coarctata* King and part with epizoic *C. dentatus*, 19.4.49 (1 + 2 small spec.); (14–19) from "Bottom net"; (14) 14 m., 27.4.51 (2 + 2 juv. dead spec.); (15) 13 m., 5.5.51, on sunken wood (1 damaged spec.); (16) 26.10.51 (numerous small clusters); (17) 12 m., 30.10.51, with bright pink stripes (3 small spec.); (18) 13.11.51, two small clusters (9 + 5 dead spec.); (19) 10 m., 9.1.52, a dead cluster (5 + 2 juv. spec.).

Nigeria: (1) Lighthouse Beach, Lagos, on cork with *B. venustus venustus* and *Chelonibia patula* (1 juv. spec.); (2) Bonny River, from No. 2 buoy at entrance to the river (1 juv. spec.); (3) the same, from buoys Nos. 3 and 4, near river mouth and from buoys between Dawes I. and Port Harcourt, many elongated through crowding and many with epizoic *B. pallidus* (numerous spec.).

The material from Ghana listed above is predominantly small and white or pale pink with lines of a deeper and often much brighter colour. The Nigerian material is older and the shells are pink with white or bluish radii. Apart from distortion due to crowding or substrate irregularities there is very little variation among the specimens which are all readily referable to the type variety.

B. tintinnabulum tintinnabulum is distributed along the whole west coast of Africa from the Mediterranean to the Cape. Off shore it occurs in the Cape Verde Archipelago (Stubbings, 1964*a* ; Hoek, 1883) and on the islands of São Tomé and Principe in the Gulf of Guinea but was not recorded from Annobon, the outermost of this island chain (Stubbings, 1961*b*). Darwin (1854) mentions Madeira. So far there appear to be no records of *B. t. tintinnabulum* from the Islands of Ascension and St. Helena.

The local distribution of *B. tintinnabulum* in West Africa depends upon the provision of a suitable substrate. Thus Sourie (1954) records it as abundant at Dakar and Conakry but absent from the friable rocks in the Cap Blanc region. In Sierra Leone, Longhurst (1958) records it from ships: presumably it will occur there also on buoys. In Ghana and in the Cameroons it is found wherever rocky shores occur (Gauld, 1957). In Nigeria it occurs on the stone breakwater of Lagos harbour and in the Niger Delta (Bonny river) on navigation buoys. The deciding factor is clearly a hard substrate.

Balanus tintinnabulum zebra Darwin

Balanus tintinnabulum var. (4) *zebra* Darwin, 1854, 195, pl. 1, fig. *g*.
Balanus tintinnabulum var. 4. *zebra:* Weltner, 1897, 260.
Balanus tintinnabulum var. *zebra:* Stubbings, 1961*a*, 21.
Balanus tintinnabulum zebra: Stubbings, 1964*a*, 108.

LOCALITY: Nigeria, Bonny river, No. 3 buoy, 14.12.57 (1 small specimen), (H.G.S. 339).

The variety *zebra* was recorded by Weltner from Walvis Bay, S.W. Africa. Gruvel (1910) records it as taken from the hull of " Gauss " on several occasions, no precise provenance being assignable. There is a suggestion that some at least settled whilst the ship was in harbour at St. Vincent, Cape Verde Is.

Specimens were taken from the hull of " Atlantide " in Lagos and in Le Havre (Stubbings, 1961*a*) and must have originated in West Africa. The same author (1963) reports specimens from Brava, Cape Verde Is. *B. t. zebra* would thus appear to occur on the west coast of Africa over a wide range of latitude in both North and South Atlantic. It is evidently much less common than the type variety.

Balanus tintinnabulum spinosus (Gmelin)

Balanus tintinnabulum var. (6) *spinosus:* Darwin, 1854, 196, pl. 1, fig. *i*.
Balanus tintinnabulum var. 6 *spinosus:* Weltner, 1897, 260.
Balanus tintinnabulum spinosus: Pilsbry, 1916, 58–59, text-fig. 10.
Balanus tintinnabulum spinosus: Nilsson-Cantell, 1932, 109.
Balanus tintinnabulum spinosus: Stubbings, 1961*b*, 184–7, text-figs. 2–4.

The known distribution of this form off West Africa was discussed by Stubbings (1961*b*). No further specimens have so far been recorded and none is known from the mainland West Coast of Africa. Nothing can be added, therefore, to the suggestion proffered in that paper that *B. t. spinosus* is an oceanic island form of *B. tintinnabulum.*

Balanus tintinnabulum crispatus (Schröter)

Balanus tintinnabulum var. (5) *crispatus:* Darwin, 1854, 195, pl. 1, fig. *h*.

Gruvel (1903) records this variety from Senegal, but there are no other old published records of this variety from West Africa and the present writer has seen none in the more recent materials examined. It must be regarded as only very doubtfully a West African barnacle.

Balanus tintinnabulum concinnus Darwin

Balanus tintinnabulum var. (8) *concinnus* Darwin, 1854, 196, pl. 1, fig. *e*, pl. 2, fig. 1*g*.

This variety is distributed on the west coast of South America (Darwin, 1854 ; Pilsbry, 1909 ; Kolosvary, 1943*a*), and is known from Siam (Broch, 1931) and New Zealand (Jennings, 1918 ; Moore, 1944). The only West African records are those of Gruvel (1903) for the Congo and Rio Muni. Pilsbry (1916) has already observed that if these records truly pertain to *B. t. concinnus* they must be based on specimens taken to those places by ship. It is unlikely that it occurs naturally in West Africa.

Balanus tintinnabulum azoricus Pilsbry

Balanus tintinnabulum azoricus Pilsbry, 1916, 62, pl. 12, figs. 2, 2*a*, 2*b*.

Pilsbry (1916) erected this subspecies to accommodate specimens from Terciera Is., Azores. It does not appear to have been identified in subsequent collections. There are resemblances to both *concinnus* and *tintinnabulum* and it may be that

Gruvel's *concinnus* from the Congo and Rio Muni is referable to this variety, in which case *B. t. azoricus* may yet be found in West African waters.

Balanus tintinnabulum **forma** ***maroccana*** **Broch**

Balanus tintinnabulum f. *maroccana* Broch, 1927, 21–22, pl. 1, figs. 4–6; pl. 2, figs. 7–8.

Broch (1927*a*) erected this forma for small specimens of *B. tintinnabulum* in which the tergal spur occupied one-half to two-thirds of the base of the valve and in which the spur fasciole was broad and shallow and never closed as in most *B. tintinnabulum*. The form was obtained well north of the tropic zone, some specimens coming from Lat. 34° 17′ N. They must be regarded as primarily warm temperate in habitat. There is a possibility, however, that specimens may be found in lower latitudes, being brought down the African coast by the Canary Current.

Balanus tulipiformis **Darwin**

LOCALITY: Off Ghana, on Kotonu-Grand Bassam telegraph cable, 55 m., 5° 25′ 45″ N., 0° E., on old shells of *B. t. tintinnabulum* pres. E. and A. Telegraph Co., B.M. 1927.8.10.6 (1 spec.).

This species is not represented in the Nigerian and Ghanaian collections here recorded, though Gauld (1957) reports its abundance off Accra in depths of more than 50 m.

B. tulipiformis has long been known as a Western Mediterranean species (Ellis, 1758; Darwin, 1854; Nilsson-Cantell, 1921, 1932*a*; Kolosvary, 1944*b*; Utinomi, 1959*a*). According to Kolosvary (1944*b*) it is absent from the Adriatic and the Black Sea. In the Atlantic it is known from Madeira (Darwin, 1854; Gruvel, 1920), Bay of Biscay (Biarritz) (Kisch, 1958, 1959), Berlengas Is. off Cape Carveiro, Portugal (Gruvel, 1912), Canary Is. (Gruvel, 1920), Rio de Oro (Stubbings, 1961*b*), Cape Verde Is. (Stubbings, 1964*a*), Senegal (Stubbings, 1965), Ghana (Gauld, 1957; Buchanan, 1957, 1958), Gulf of Guinea (Principe Is.) (Stubbings, 1961*b*), Congo estuary (Stubbings, 1964*b*) and Angola (Stubbings, 1961*a*). This last in Lat. 8° 30′ S. is the most southerly record of the species. There is no record of *B. tulipiformis* from South-west Africa or the Cape of Good Hope, neither has it been recorded from the South Atlantic islands of Ascension and St. Helena.

There are no western Atlantic records of the species and apart from Gruvel's (1907*a*) record from Wasin Is., E. Africa there is none from the Indian Ocean. The geographical range of *B. tulipiformis* is confined to the eastern Atlantic from about 43° 30′ N. to 8° 30′ S. and the Western Mediterranean basin. It is a sublittoral species occurring in depths of from 25 to 250 m.

Balanus nigrescens **Lamarck**

This Australian–West Pacific species is recorded from San Pedro, Ivory Coast by Gruvel (1903). There are no other records of the species occurring naturally in the Western hemisphere. It is found occasionally as a fouling species on ships (Wood and Allen, 1958) and Kruger (1927) records dead specimens removed from a ship's hull in Copenhagen. It is possible, therefore, that the Ivory Coast specimens were originally obtained from a hull, though Gruvel does not mention any substrate. Mme. Davadie (1963) has published photographs of the opercular valves of the Ivory Coast material from which it would appear that the identification is unquestionable. The real status of *B. nigrescens* in West Africa is therefore uncertain.

Balanus maxillaris Gronovius

The geographical distribution of *B. maxillaris* appears to be centred on the southern extremity of Africa from which it extends into sub-Antarctic waters (Nilsson-Cantell, 1939*a*). It has not been recorded from tropical West Africa, but there are records from Port Etienne, Morocco (Nilsson-Cantell, 1939*b*) and Luderitz Bay and Swakopmund in S.W. Africa (Kolosvary, 1943*a*, *b*). It is possible that these occurrences are due to shipborne introduction of the species. Both the northern and southern localities cited lie within areas influenced by equatorward cold currents and it is possible, therefore, that under these influences the species may extend further towards the equator in both hemispheres.

Balanus trigonus Darwin

Balanus trigonus Darwin, 1854, 223–4, pl. 3, figs. 7*a–f*.

LOCALITIES: Gambia: (1) off Gunjur from hull of shark-fishing boat, on *B. t. tintinnabulum*, 3.3.51, coll. M. H. Routh, B.M. 1952.10.2.3 (few juv. spec.); (2) from seawater intake of "African Queen", on *B. t. tintinnabulum*, 2.10.51, coll. M. H. Routh, B.M. 1952.10.2.5 (2 juv. spec.).

Sierra Leone, (1) 12.1.52, coll. A. R. Longhurst, B.M. 1957.6.3.5 (19 dead spec.); (2) coll. on board S/T "Cape St. Mary" P. H. Creutzberg, pres. A. R. Longhurst, B.M. 1956.1.7.11 (9 dead and 1 live spec.).

Balanus trigonus is of world-wide distribution in tropical and subtropical waters. In the Atlantic it occurs from the Azores and Madeira to the Cape of Good Hope in shallow water. It is present in the Mediterranean. On the African Mediterranean Coast there are records from Oran (Kolosvary, 1943*a*). It was not reported by Broch (1927) from the Atlantic Coast of Morocco but Gruvel (1912) states that it occurs on all the Atlantic Coast of the Sahara (i.e. Mauretania). Sourie (1954), also reports its abundance at Cap Blanc, Mauretania and at Dakar, Senegal. It is very common on the Senegal Coast (Stubbings, 1965) and was present in almost all the "Calypso" collections made in the Cape Verde Archipelago (Stubbings, 1963).

From south and east of Senegal there are very few records. Longhurst (1958) obtained it twice only in his survey of the benthos off Sierra Leone. There are no records from Liberia, the Ivory Coast or Ghana and only one from Lagos, Nigeria (Stubbings, 1961*a*). From Liberia this lack of records may be due to lack of investigations but the absence of the species from Ghana must be real in view of the extensive collecting by Bassindale. It was not found among the islands of the Gulf of Guinea.

South of the Bight of Biafra records are again more frequent and *B. trigonus* is recorded down to Tiger Bay on the southern border of Angola (Gruvel, 1912). There is a single record from Great Fish Bay, South-west Africa (Weltner, 1922). In this paper Weltner reports the species from various localities in the Cape and Barnard (1924) states that it is found all round the South African coast from False Bay to Zululand.

It would appear, therefore, on present information that *B. trigonus* is common on the N.W. Atlantic coast of Africa, it being most abundant in the Senegal–Cape Verde area. From about 10° N. to 5° S. it is evidently uncommon. Collecting on the coasts of Angola, South-west Africa and the western coast of the Union has not been intensive, largely due to difficulties of access, but such records as we have would indicate that *B. trigonus* is present throughout this section of the coast. It is evidently common on the southern coast of the Union and well into the Indian Ocean.

Balanus spongicola Brown

B. spongicola is not contained in the present collections. It is widespread in the eastern Atlantic and Western Indian Ocean. In West Africa there are records from French Guinea (Stubbings, 1961*a*), Rio de Oro and Ghana (Stubbings, 1961*b*) and Angola (Stubbings, 1963). It is known from the western Mediterranean, Algiers (Darwin, 1854) and Catania (Kolosvary, 1943*a*). Northwards it extends to Portugal (Kolosvary, 1943*a*), Madeira (Darwin, 1854), the Azores (Gruvel, 1920) and the south-west coast of England (Darwin, 1854; Norman & Scott, 1906).

The identity of *B. dollfusi* Broch (1927*a*) with *B. spongicola* has been discussed by the author (Stubbings, 1963) elsewhere. All records of this species in the literature refer to localities whence *B. spongicola* has been collected or are within its known geographical range, namely the Atlantic coast of Morocco (Broch, 1927*a*) Rio de Oro (Nilsson-Cantell, 1939*b*) and off the Congo estuary (Nilsson-Cantell, 1938*b*).

Gruvel (1907*b*, 1910) records it from Simonstown, South Africa and Barnard (1924) from numerous places from False Bay to Zululand. In the Indian Ocean it is found in the Chagos Archipelago and Seychelles (Gruvel, 1907*a*). Kolosvary (1943*a*) cites specimens in Budapesth from the East Indies, but there are no other records from this region and confirmation by new material is desirable.

Darwin (1854) placed some specimens from the West Indies in an unnamed variety, but was uncertain as to their true status. Pilsbry (1916) elevated these to specific status as *B. calidus*. It is probable that the W. Indian and tropical American material recorded as *B. spongicola* by Weltner (1897), Nilsson-Cantell (1927) and Kolosvary (1943*a*) should be assigned to Pilsbry's species, though in neither of the two last cited works does the author mention *B. calidus*.

Balanus perforatus Brug.

This species is not represented in the Ghanaian or Nigerian materials here reported. Recent records of the species in West Africa are from the southern portion of its range, south of the Bight of Biafra : Fausse Pointe Noire (Congo) (Stubbings, 1964*b*) and Lobito and Moita Seca, Angola (Stubbings, 1963).

B. perforatus exhibits the same divided distribution in West Africa as does *B. trigonus*. There are a number of records from Morocco and Mauretania (Broch, 1927*a* ; Gruvel, 1912) and the Canary Islands (Nilsson-Cantell, 1932*a*). Darwin names the Gambia as a locality and Bruguière (1789) cites Senegal in his original description, but there are no other localities recorded to the southward until Pointe Noire in Congo (formerly French Equatorial Africa) is reached. The species is unknown from south of Senegal to the southern border of the Gulf of Guinea. There are several records from the Congo and Angola but it has not been found on the south-west coast south of Lobito, Angola. Gruvel (1907*b*, 1910) records the species from rocks at Simonstown, South Africa.

The cited records include references to the vars. (or formae) *angustus* and *fistulosus*, both being growth forms, the former occurring where erosion is slight, the latter due to overcrowding. The collected and recorded material of *B. perforatus* from West Africa is unsatisfactory in that much of it consists of empty shells, dead when collected. There is, therefore, an element of doubt as to the true status of the species in some of the recorded localities. Dead shells may be the remains of an indigenous species, be derived from imported specimens that have bred but not been able to maintain themselves, or be merely the remains of imported shipborne specimens. It is probable that many of the present records represent shipborne introductions that have failed to maintain themselves for more than a short period. Until much more living material, preferably in clusters comprising individuals of various ages, is available, there must remain an element of doubt regarding the true status of *B. perforatus* in West Africa. In any case, it seems safe to presume its absence from about Lat. 10° N. to 5° S.

The geographical limits of *B. perforatus* beyond south-west Europe and the west coast of Africa are somewhat debatable. Its general distribution in the Mediterranean is undisputed and Zevina & Tarasov (1954) have recorded it, as a new record for Russian waters, in the Black Sea. In the eastern North Atlantic it extends to south-west England and South Wales (Norris & Crisp, 1953), though it is absent from the Scilly Isles (Fischer-Piette, 1936). It was not found by Southward & Crisp (1954) in their survey of the intertidal fauna of the Irish coastline but Williams (1954) records it from about 20 m. in Strangford Lough. Occasionally, therefore, it may penetrate far into St. George's Channel. The Scottish record from the Jeffrey's collection (Pilsbry, 1916) is of doubtful validity as is even more so that from Kirkeness in Gruvel (1903).

Darwin hesitated to accept Western Atlantic records for *B. perforatus* and in this he was followed by Pilsbry (1916) on the grounds that they had not been confirmed by later records although Weltner (1897) cites specimens of the var. *angustus* on " *Purpura haemastoma* " from Brazil in the Berlin Museum. Nevertheless there are no recent records of western *B. perforatus* and its occurrence on both sides of the Atlantic must still be regarded as equivocal. The Andaman Islands record in Gruvel (1907*c*) must be in error. The author himself admits that the specimen was scarcely recognisable.

Balanus eburneus Gould 1841

LOCALITY: Accra, on boat buoy, 14.1.51 (2 spec., 1 damaged).

This is the only example of this species in the collection. The intact specimen measures 11·5 mm. carino-rostral diameter as compared with 14–15·5 mm. for material from Woods Hole, Mass., and is therefore not quite full-grown. The specimens are quite typical of *B. eburneus* in shell and valve structure.

This American species has been recorded in the Old World on many occasions since first being reported by Ostroumoff (1892) from Sevastopol, Black Sea. Fischer-Piette & Prenant (1956) have summarized records of *B. eburneus* in the Black Sea and at Istanbul and give many localities on the Atlantic coast of North Spain. Its occurrence in the Adriatic has been reported by Kolosvary (1941*a*, 1944*a*, *b*) and in the Mediterranean by Bishop (1951) and Nilsson-Cantell (1938*a*). Fischer-Piette & Prenant (1957) were surprised not to find *B. eburneus* in Portugal, south-west Spain or Morocco. There are no records for the West African coastline other than the above record from Accra. Its rarity suggests that it is not yet established on the West African coast but is occasionally imported in a breeding condition on ships.

Balanus improvisus Darwin

Balanus improvisus has a vast geographical distribution. Its presence on West European coasts and in the Mediterranean and Black Sea is amply documented, as is its presence on the Atlantic seaboard of North America. In the Tropical and South Atlantic there are a number of records from the West Indies (Darwin, 1854; Pilsbry, 1916; Henry, 1959) but fewer from the coast of South America, (Darwin, 1854; Weltner, 1897; Borradaile, 1916) and from West Africa. Broch (1927*a*) recorded *B. improvisus* from Morocco and Gruvel (1907*b*) from the Cape of Good Hope and (1912) from the Congo estuary. It was not present in collections reported on by the writer (1961*a*, *b*, 1963, 1964*a*, *b*). It would appear, therefore, that *B. improvisus* is not common on the west coast of Africa. It is commonly transported by ships and records from estuarine areas such as the Congo, where not collected from ships' hulls, may represent shipborne introductions that have perished, or at least not multiplied greatly. It is evident that *B. improvisus* has not established itself in quantity as it has for instance in the Bosphorus (Neu, 1935, 1939) and in Japan where it has appeared in recent years (Kawahara, 1961, 1963).

Balanus improvisus var. *assimilis* Darwin

This variety of *B. improvisus* occurs in warm water and does not appear north of the Mediterranean whence it has been recorded by Gruvel (1903). It is known from the West Indies (Gruvel, 1903; Darwin, 1854; Nilsson-Cantell, 1928) and from Brazil (Weltner 1897). In the eastern Atlantic there are records from Mauretania and the Congo (Gruvel, 1912) and Bishop (1951) records specimens on ships coming from West African ports under circumstances suggesting that settlement took place there.

The possibility that white forms of *B. amphitrite* might be confused with *B. improvisus* var. *assimilis* prompted a re-examination of much of the white " *amphitrite* " material to hand. No *improvisus* were found, the white " *amphitrite* " examined all proving to be thin-walled specimens of *B. pallidus* Darwin (= *B. a. pallidus* Darwin). These thin white forms all had opaque white lines opposite the internal ribs of the paries with thin, clear areas between, whereas Darwin expressly states that the translucent areas in *B. improvisus* var. *assimilis* correspond to the longitudinal parietal septa. The identity of the specimens was confirmed by the very long *pallidus*-type spur to the tergum.

There can be no doubt, therefore, that this variety of *B. improvisus* is far from common in West Africa.

Balanus amphitrite Darwin

In considering *B. amphitrite* I have followed Harding (1962) in nomenclature. Hence the Darwinian varieties *venustus*, *pallidus* and *stutsburi* are dealt with separately, the first as *B. venustus* and the other two as *B. pallidus*. The varieties *communis* Darwin, *hawaiiensis* Broch and *denticulata* Broch are combined as *B. amphitrite amphitrite* Darwin.

Balanus amphitrite amphitrite Darwin

Balanus amphitrite Darwin, 1854, 240, pl. 5, figs. 2*e*, *h*, *l*.
Balanus amphitrite hawaiiensis: Utinomi, 1960*a*, 43, text-figs. 1–3.
Balanus amphitrite amphitrite: Harding, 1962, 274, pls. 1, 2.

LOCALITIES: Gambia: from seawater intakes of " African Queen ", with *B. pallidus* and *B. trigonus* on *B. t. tintinnabulum*, 2.10.51, coll. M. H. Routh, B.M. 1952.10.2.5 (several spec.).

Sierra Leone: Kissy, Sierra Leone River (1) infra-littoral fringe on rocks, 19.7.55, coll. A. R. Longhurst, B.M. 1956.1.7.9 (19 spec.): (2) on bakelite panel exposed 22.3.54–14.6.54, a heavy encrustation (H.G.S.).

Ghana: (1) Ankobra ferry, on logs with *C. dentatus*, 19.2.49 (many spec.); (2) the same, on copper sheathing of boat with epizoic juv. *B. tintinnabulum* (1 spec.); (3) Accra, on boat buoy, 14.1.51 (15 spec.); (4) Labadi, Accra, on gastropod shell; 22.3.58 (9 dead spec.) (H.G.S.); (5) Kpeshie Lagoon, Accra, on oyster shell, coll. D. T. Gauld (38 spec.).

Nigeria: (1) Port Harcourt on hull of launch, (52 juv. spec.) (H.G.S.); (2) Opobo, Imo River, from concrete boat slipway (8 spec.) (H.G.S.).

Considerable confusion has arisen over the identity of the forms variously regarded as varieties or subspecies, *B. amphitrite communis* Darwin (1854), *hawaiiensis* Broch (1922) and *denticulata* Broch (1927*b*) doubtless stemming from the sketchy description of the earliest described. Utinomi (1960*a*) advanced reasons for regarding *hawaiiensis* and *denticulata* as identical, the former name having priority. At the same time Utinomi listed the criteria for distinguishing *B. a. hawaiiensis* from Darwin's var. *communis*.

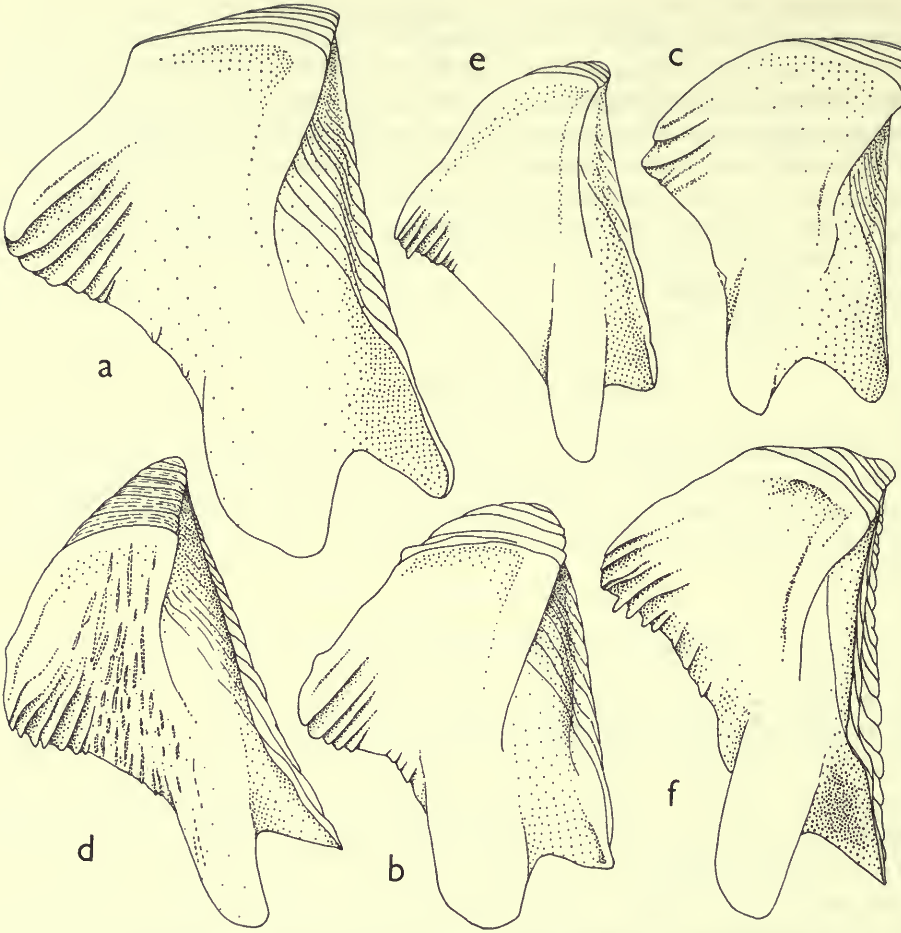


FIG. 14. *Balanus amphitrite amphitrite* Darwin : internal views of terga of six specimens ; *a*, removed from hull of " Atlantide " at Le Havre ; *b*, Kpeshie Lagoon, Accra ; *c*, Labadi, Accra ; *d*, Freetown, Sierra Leone ; *e*, *f*, Lagos, Nigeria (" Atlantide " Sta. 93) ; (*a*, *c* ×28 ; *b*, *d–f*, ×14).

Harding (1962) has given a much-needed re-description of the original Darwin specimens. From this it is evident that the Darwinian var. *communis*, bearing the name in his handwriting, has the characters usually ascribed to *denticulata* or *hawaiiensis* by later authors, and just those listed by Utinomi as typical of *hawaiiensis* and distinguishing it from *communis*. The Darwinian name has clearly become associated with the wrong set of characters, through lack of sufficiently precise information on the original material. Hence, presupposing *communis* and *hawaiiensis* to be distinct, specimens conforming to Utinomi's summary of *hawaiiensis* characters should be termed *B. a. communis* Darwin, or in modern terminology *B. amphitrite* var. or ssp. *amphitrite* Darwin. Those with the characters listed by Utinomi for *B.*

amphitrite communis, if distinct, cannot bear this name but must receive a new varietal or subspecific epithet.

Before taking such action it is prudent to consider whether the apparently clear-cut distinctions between "*communis*" and "*hawaiiensis*" in Utinomi (1960*a*) can be maintained in practice. Material referable to these forms has been gathered from the thirteen localities named below and examined for these supposedly diagnostic characters:

Bathurst, Gambia
Freetown, Sierra Leone
Labadi
Kpeshie Lagoon } Ghana
Ankobra Ferry
Lagos, Nigeria
Zwartkops R., S. Africa
Inhaca Is., Mozambique
Izmir, Turkey
Haifa, Israel
Kuwait
Le Havre, France
Devonport, England

The most clear-cut character, after dissection, is the number of teeth on the labrum. In the 28 specimens examined the smaller numbers found varied from as few as two/three (on the two halves) in a specimen from Lagos to 4 or 5, all widely spread and all on the anterior border close to the edge of the median notch. Only the tooth nearest the mid-line was seated in the notch itself. There was then a jump to 8 or 9, or more teeth, of which many were situated in the notch in the typical close-set "*denticulata*" manner. A clear distinction is evident between a labrum with a few teeth (2 to 5) and another with numerous teeth (8 or 9 or more).

According to Utinomi (1960*a*) the number of parietal tubes in the rostrum is significant, there being about 16 in *denticulata* and only about 9 in *communis*. Using the same specimens, the number of tubes varied from 11 to 21, never as low as nine. The two with only 11 rostral parietal pores had numerous teeth on the labrum. Specimens from all "tube No. categories" had numerous teeth on the labrum. Only "three" (2–5) such teeth occurred in specimens with 12–17 rostral pores. There is no relation between number of rostral pores and number of labral teeth.

The tergal features of spur shape and proportions and number of depressor crests are easy to observe. According to Utinomi in *denticulata* the spur is broad, over one-third the width of the basal margin of the valve, short and rounded or truncate distally, less than its own width from the basiscutal angle. In *communis* it is said to be longer than wide, and separated by its own width from the angle. Utinomi figures both forms (1960*a*, text-figs. 2*a*, *c*) though here the differences are not so marked as some that occur. Forms of "*denticulata*" type tergum occur with a much broader spur (see for instance the lectotype of *B. amphitrite amphitrite* in Harding (1962) pl. 1, figs. *e*, *f*). The length of the spur also is variable. According to Harding (1962) a few of the specimens labelled "*communis*" by Darwin have the tergal spur narrow as figured by him (1854, pl. 5, fig. 21) but the majority of Darwin's specimens have a broad spur. A series of six terga of specimens from various localities (Text-fig. 14) shows this range of spur form. The first two (Text-fig. 14*a*, *b*) show the broad tergal spur, comparable to that of the lectotype ; in *c* it is reduced in width and in *d* and *e* is so narrow as to be longer than broad. The specimen *f* has a similar narrow spur. Here the margins are roughly parallel and the spur is more sharply marked off from the basal margin of the valve.

Occasionally terga (and scuta) are thin, so that the growth lines are faintly visible internally. More often they are more heavily calcified and are opaque with a smooth internal surface. Roughened areas occur on some terga and rarely may cover the whole internal surface (Text-fig. 14*d*). The depressor muscle crests are very variable in number and development. Five or six well-developed crests appears to be the normal number with one or two very short and ill-defined crests nearer the spur. The outer crest or crests towards the carinal margin of the valve are often less sharply defined (e.g. Text-fig. 14*d*, *e*). Additional small ill-defined crests may be present on the basal margin, e.g. Text-fig. 14*b* and *f*. Text-fig. 14*c* shows a tergum with very poorly developed crests, only two rather low crests being present with very faint traces of a further two inside these.

By plotting the distribution of pairs of characters it is possible to see how far they are linked, even when the separate characters are not expressed numerically. Thus radii with horizontal tops are associated almost exclusively with numerous teeth on the labrum (Text-fig. 15*a*), but oblique radii may be associated about equally with few or numerous labral teeth. There is better correlation between form of radii and form of spur (Text-fig. 15*b*) : a narrow radius with oblique summit appears to be associated exclusively with the longer and narrow tergal spur. A broad spur was not found with this type of radius. But the broad radius with horizontal top is not associated only with a broad spur. In one-third of the admittedly small sample of 12 specimens, the spur was definitely longer than broad. The number of well-developed depressor crests on the tergum (Text-fig. 15*c*) is on average higher (6·43) on forms with narrow oblique radii than on forms with broader radii with horizontal summits (4·9). Similarly the average number of crests is higher where the spur is narrow (*e*) or there are few labral teeth (*f*). A broad spur is almost always associated with numerous labral teeth (*d*) but the converse does not hold (cf. radii and labral teeth in (*a*)). Forms with a narrow-spurred tergum and few or many labral teeth occur with equal frequency.

We can thus pick out a set of features characterizing a " well developed " type of animal, viz : broad radii with horizontal summits, broad tergal spur, numerous labral teeth and 5 depressor crests (or occasionally less) on the tergum. This is, in fact, the result arrived at by Utinomi (1960*a*) and the above features characterize his interpretation of *B. a. hawaiiensis* Broch (= *denticulata* Broch).

The opposite characters—narrow radii with oblique summits, a narrow and longer tergal spur, and few teeth on the labrum and more than 5 depressor crests on the tergum also occur in association. These are the characters, again among others, listed by Utinomi for *B. a. communis* Darwin. But, as the diagrams in Text-fig. 15 indicate these associations are not constant—a narrow tergal spur, or narrow radii occur as frequently associated with numerous labral teeth. Hence, specimens occur with a " mixed " assemblage of characters and the question arises as to which of these must be regarded as determining the name to be assigned to the specimen. Of the

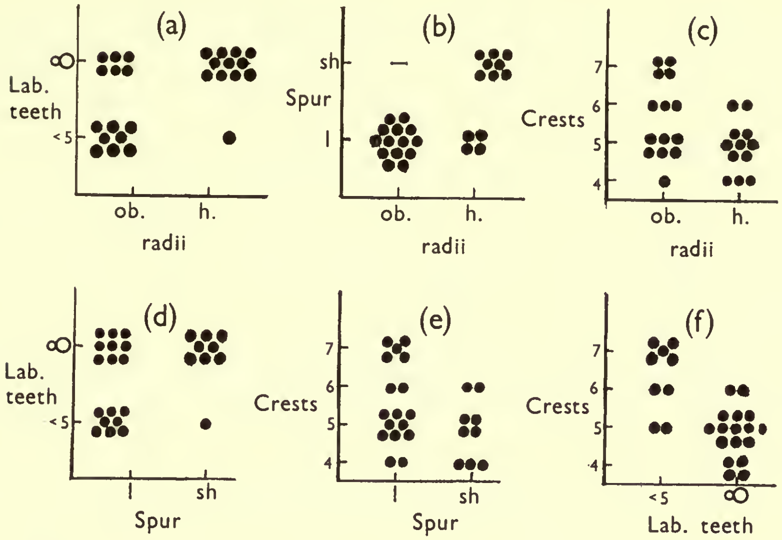


Fig. 15. Frequency of occurrence of various pairs of characters in *B. amphitrite amphitrite* Darwin, namely: radii with oblique (ob) or horizontal (h) summits; tergal spur short and broad (sh) or longer and narrow (l); number of depressor muscle crests on tergum; and labral teeth five or less, or numerous.

26 specimens examined in detail no less than eight were in this mixed category. The mixed range of characters found is typified by the following examples:

(1) Kpeshie lagoon, Ghana (Text-fig. 14*b*): radii broad, horizontal summits: tergal spur broad, 5 tergal crests (= "*denticulata*"), *but* labral teeth only 4/5 on the two sides.

(2) Bathurst, Gambia: radii narrow, tergal spur long and narrow (= *communis*) *but* tergal crests 4 and labral teeth numerous (= *denticulata*).

(3) Four specimens from the same Lagos gathering had the following characters: radii narrow, with oblique summits, spur narrow, and (*a*) tergal crests 5: labral teeth 8 or 9. (*b*) tergal crests 5: labral teeth c. 12. (*c*) tergal crests 6/7[1]: labral teeth 3. (*d*) tergal crests 5 (+1)[2] labral teeth 2/3.

Specimens 3 (*a*) and (*b*) are anomalous, (*c*) and (*d*) are assignable to "*communis*". The first two were white-shelled and without pigment, a character not quoted by Utinomi for either group. The second two have shells with a pinkish or flesh tint and pale purplish lines, which fits with Utinomi's description.

The colour of the shells calls for comment. Utinomi characterizes "*hawaiiensis*" as having a glossy white shell with dark violet longitudinal stripes, some being reduced or absent: "*communis*" is regarded as "rather reddish white, darkened with bluish tint in upper part" with "pale or dark violet longitudinal stripes crossed by the same, coloured or reddish transverse stripes on the whole area". At least as far as the Mediterranean and West African specimens are concerned, this also is a

[1] 6/7 etc. on the two valves or sides of labrum.
[2] 5 (+1), 5 crests + 1 rudimentary crest.

perfectionist view. I have seen East African specimens with near white shell and the dark pigmented (purple rather than violet) lines arranged as described. But West African shells most often bear only pale stripes of a dull faded purple or pale reddish colour, the latter often regularly interrupted by still paler horizontal lines. Vertical lines may be absent from one or more sectors of the paries regardless of intensity of line colour. In a considerable proportion of shells all colour is absent. I cannot agree that all specimens can be resolved into those with dark lines interspersed with white sectors and those with regularly arranged paler or interrupted lines and no white sectors. Too many lightly pigmented specimens have white shell sectors.

There is thus a high proportion of specimens ostensibly with characters of both varieties or subspecies, and which cannot readily be assigned to one or the other. Each of these same characters varies in degree of development, so that for many of them there is a complete gradation from one varietal form to the other. Thus it becomes difficult, if not impossible, not only to place many specimens in a " variety " but also to state categorically to which varietal type a particular character may be assigned. Under these circumstances it is preferable to regard the various characters described as randomly variable within the " *communis* "–" *hawaiiensis* " complex and not segregating in a clear cut manner such as to allow of the characterization of true varieties.

Within purely local populations a greater uniformity may prevail. The encrustation of specimens on a panel exposed at Freetown is of this type. There is considerable uniformity among individuals. But these are from one small locality and all living at one time (within a 3-month period). This resemblance among individuals of a group collected in one place appears usual—but it does not apply automatically to specimens from other places, even those nearby, or to collections at other times.

It is, therefore, preferred, to regard the West African *B. amphitrite*, previously described variously as *communis*, *denticulata* or *hawaiiensis* as one rather variable form only, to which the name *B. amphitrite amphitrite* Darwin is applicable.

B. amphitrite amphitrite occurs as far north as the western English channel in places where conditions are exceptionally favourable. It occurs intermittently on the Atlantic coasts of France and the Iberian peninsula (Bishop, Crisp, Fischer-Piette & Prenant, 1957). It appears to be absent from the Straits of Gibraltar and to occur intermittently on the Spanish shore of the western Mediterranean (Barnes & Barnes, 1964). Utinomi (1959*a*) does not record it from Banyuls nor from the coast of Algiers (1959*b*) but the material recorded in the latter paper is all from off-shore, so the absence of this shore or shallow water species from Algiers is not proven. Broch (1927*a*) likewise, does not report it from the Atlantic coast of Morocco.

The same intermittent occurrence, usually in very small numbers is found on the west coast of Africa and in the off-shore islands. It occurs in the Canary Islands (Stubbings, 1963) but was not found in the Cape Verde Islands (Stubbings, 1964*a*) or in the islands of the Gulf of Guinea (Stubbings, 1961*b*). On the African mainland there is a record from Port Etienne, Mauretania (Broch, 1924*a*) and others from Senegal (Stubbings, 1965) Gambia (Stubbings, 1961*a*) Portuguese Guinea (Stubbings, 1965) and Sierra Leone. On this extreme western sector of the West African coast it appears at its most abundant. It is particularly common in the Sierra Leone estuary. Further east and south there are a few records of small numbers from Ghana and Nigeria and one record of a group of specimens from Angola (Stubbings, 1964*b*).

Balanus amphitrite var. ***albicostatus*** Pilsbry

B. a. albicostatus Pilsbry, 1916, 90, pl. 20, figs. 1–4.
B. a. albicostatus: Kolosvary, 1943, 84.

This variety, originally described from Far Eastern specimens has been recorded once from the Mediterranean (Catania) and once from Senegal, West Africa, (Kolosvary, 1943*a*) but from nowhere else on the Eastern Atlantic seaboard. In view of the large amount of West African barnacle material now available the lack of later records casts doubt on this earlier record and the status of *B. a. albicostatus* as a member of the West African fauna is suspect.

Balanus pallidus Darwin

Balanus amphitrite var. (3) *pallidus* Darwin, 1854, 240, pl. 5, figs. 2*c*, *k*.
Balanus amphitrite var. (6) *Stutsburi* Darwin, 1854, 240, pl. 5, figs. 2*d*, *i*, *m*, *n*, *o*.
Balanus dybowskii Gruvel, 1903, 143–8, pl. 1, figs. 1–9; pl. 4, fig. 14.
Balanus pallidus pallidus: Harding, 1962, 278, pl. 3.
Balanus pallidus stutsburi: Harding, 1962, 281, pl. 4.

LOCALITIES: Gambia: from sea-water intake of " African Queen ", pure white shells on *B. tintinnabulum* with a few *B. trigonus* and *B. amphitrite*, 2.10.51, pres. M. H. Routh, B.M. 1952.10.2.5 (numerous spec.).

Sierra Leone: (1) Sierra Leone River, 20 m., 5.12.54, coll. A. R. Longhurst, B.M. 1956.1.7.6; (2) S. Leone River, 2 clusters 13.10.54, coll. A. R. Longhurst, B.M. 1956.1.7.8 (10 + 5 spec.); (3) Kumrabe Creek, S. Leone River, 2 m., on *Pachymelania aurita*, 2.12.52, coll. A. R. Longhurst, B.M. 1956.1.7.7 (1 spec.).

Ghana: (1) R. Densu on mangrove 0·5 mile from sea, 3.4.49 (53 spec.); (2) on launch " Akuse ", Ada, R. Volta, 15.3.49 (193 spec.); (3) on stranded pontoon, Ankobra, 19.2.49 (several dead spec.); (4) Christiansborg, Accra, 19.11.49 (1 dead spec.); (5) Chorkor, Accra, –.3.49 (12 spec.)

Nigeria: (1–4) Lagos: (1) from test panels, Tarquah Bay, 19.10.57 (56 juv. spec.) (H.G.S. 235); (2) the same, 21.10.57 (218 spec.) (H.G.S. 240); (3) the same, 21.6.54, coll. T.T.E. staff (7 spec.); (4) Wilmot Point, n.d., coll. T.T.E. staff (27 + 17 dead spec.); (5–19) Port Harcourt: (5) police wharf, 11.9.57 (5 spec.) (H.G.S. 156); (6) raft, 19.9.57 (12 spec.) (H.G.S. 179); (7) raft, 28.9.57 (5 spec.) (H.G.S. 200); (8) raft, 9.10.57 (30 spec.) (H.G.S. 217); (9) raft, 5.11.57 (21 spec.) (H.G.S. 283); (10) raft, 21.11.57 (94 spec.) (H.G.S. 307); (11) raft, no data (13 spec.); (12) on mangrove roots, 29.10.57 (33 spec.) (H.G.S. 252); (13) on steel launch, 28.10.57 (52 juv. spec.) (H.G.S. 257); (14) from test-frames on " dolphin ", 6.10.55 coll. T.T.E. staff (7 spec.); (15) on *Ostrea* sp. on " dolphin ", 20.11.57 (9 spec.) (H.G.S. 294); (16) the same, 19.12.57 (42 spec.) (H.G.S. 348); (17) on " dolphin ", 19.12.57 (46 spec.) (H.G.S. 349); (18) on *Ostrea* sp. on " dolphin " 19.12.57 (4 spec.) (H.G.S.

342); (19) on "dolphin" 18 in. above extreme L.W. 19.12.57 (4 spec.) (H.G.S. 351); (20) Nigerian Ports authority, dockyard pier, 11.12.57 (89 spec.) (H.G.S. 329); (21–26) Bonny River Buoys: (21) between Dawes I. and Port Harcourt, 30.10.57, (43 spec.) (H.G.S. 259); (22) No. 2 buoy, 11.12.57 (4 spec.) (H.G.S. 327); (23) No. 3 buoy 11.12.57 (1 spec.) (H.G.S. 339); (24) the same (5 spec.) (H.G.S. 340); (25) No. 4 buoy, on *B. tintinnabulum*, 11.12.57 (4 spec.) (H.G.S. 402); (26) No. 5 buoy, 14.12.57 (8 spec.) (H.G.S. 342); (27–29) Bonny: (27) old iron pier, 28.11.57 (27 spec.) (H.G.S. 320); (28) the same (17 spec.) (H.G.S. 322); (29) new concrete pier, 28.11.57 (32 spec.) (H.G.S. 324); (30–32) Opobo, in Imo River; (30) 9.8.53, coll. T.T.E. staff (many spec.); (31) on jetty, 11.1.58 (53 spec.) (H.G.S. 373); (32) on Eastern Region Development Commission concrete boat slip, 31.1.58 (8 spec.) (H.G.S. 372); (33) Oron, Cross River, on *Thais* sp. and *Brachiodontes niger*, 17.2.54, coll. T.T.E. staff (numerous spec.).

Cameroon: Bota, Ambas Bay, on concrete boat slip, 21.2.58 (1 spec.) (H.G.S.) 428).

The Darwinian varieties *B. amphitrite* var. *pallidus* and var. *stutsburi* are included under this name. A great deal has been written on the variability of form and the status of these two varieties.

The identity of *B. dybowskii* Gruvel with *B. a. pallidus* was recognized earlier (Stubbings, 1963). Suffice it to say here that many of the estuarine samples, notably those from Opobo on the Imo River contain *dybowskii*-like specimens. The absence of radii is due to heavy erosion of specimens with originally narrow or rudimentary radii. Apart from surface erosion the apices of compartments are much worn down so that the shell becomes a low eroded calcareous ring with no external features.

The extent of pigmentation of *B. pallidus* varies from complete coverage of the compartments, through intermittent horizontal bands of colour to a single narrow band on either side of the paries of a compartment and finally to a complete absence of the purple pigment. In any gathering of specimens from a locality there is considerable colour variation often extending from wholly white specimens to those with much colour. Completely pigmented specimens such as that figured by Darwin (1854, pl. 5, fig. 2*d*) as var. *stutsburi*, are not common. Miss Sandison (1962, 541) found that white compartments were more common in barnacles that settled during the dry season and purple-marked shells in those that settled in the wet season. Colour is thus a matter of seasonal growth, and probably of food supply, as Miss Sandison suggests, and is of no systematic significance.

The shapes of terga from several sites in Nigeria have been illustrated by Miss Sandison (1962, text-fig. 4). A further selection of terga from Gambia, Ghana and two sites in Nigeria is shown in Text-fig. 16. The Bathurst, Gambia specimen (Text-fig. 16*a*) is similar to her Port Harcourt example, whilst the present Port Harcourt specimen (Text-fig. 16*e*) is more like her Tiko, Cameroon specimen in its narrow spur and its basal emargination. The Tarquah Bay, Lagos specimens (Text-fig. 16*c*, *d*) are very like her lower Lagos tergum except that the spur is narrower and slightly hooked. Tarquah Bay is situated at the seaward end of Lagos harbour.

There is a similar range of variability in the scuta and specimens paralleling those shown by Miss Sandison (1962, text-fig. 5) are not difficult to find.

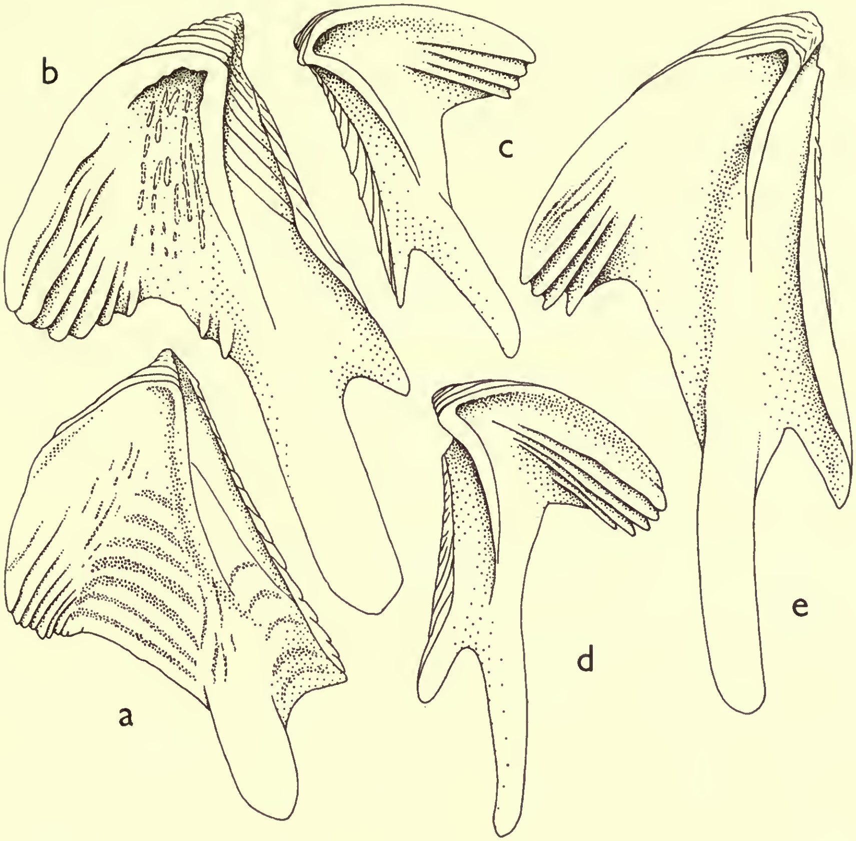


FIG. 16. *Balanus pallidus* Darwin: terga of five specimens; *a*, from Bathurst, Gambia (" Atlantide " Sta. 155) with rather short spur and straight basal margin; *b*, from Ada, R. Volta, Ghana (coll. R. Bassindale) with long, stout spur and some excavation of basal margin; *c*, *d*, two lightly calcified thin specimens from Tarquah Bay, Lagos, Nigeria (coll. H.G.S.) with long slender spur and deeply excavated basal margin; *e*, a more heavily calcified specimen than the preceding from the mooring " dolphin " at Port Harcourt, Nigeria, (coll. H.G.S.), with long, stouter spur and concave basal margin (all ×14).

B. pallidus is the predominant species in all the estuaries, extending from the river mouth well up the rivers where salinity may be reduced very considerably during the rainy season. At Port Harcourt, for instance, where *B. pallidus* is always present, the salinity falls to 12‰ or slightly lower late in the rains. Where salinity falls very low, however, *B. pallidus* is seasonal only, as in Lagos Harbour (Sandison, 1962). Its absence from the Cross River at Calabar (Sandison 1962 and personal observation) is explanable on low salinity, for the river there is virtually fresh at all times. In February, 1958, a salinity of only 0·01‰ was recorded (personal observation). Lower down the Cross River, at Oron, it occurs as in other and smaller estuaries.

B. pallidus is rare on the open coasts. The single specimen recorded above from

Christiansborg, Accra, is exceptional. It was dead and may well have been carried by the tide and surf from elsewhere.

Miss Sandison (1962) noted that east of Accra the only suitable area for *B. pallidus* should be the mangrove areas of the Volta estuary. Gauld (1957) had already recorded it from Angaw Creek in that area and the present record from Ada confirms this locality. West of Accra we now have records from the estuaries of the rivers Densu and Ankobra.

On the West African coast as a whole, *B. pallidus* is known from Fedhala, Morocco (Broch, 1927) to the Congo estuary (Weltner, 1922 ; Nilsson-Cantell, 1938*b* ; Stubbings, 1963). There is a record of a single specimen from the Cape Verde Archipelago (Stubbings, 1964*a*) but the species appears to be rare there.

Balanus venustus venustus Darwin 1854

Balanus amphitrite var. (2) *venustus* Darwin, 1854, 240, pl. 5, fig. 2*a*.
Balanus amphitrite var. 2, *venustus;* Weltner, 1897, 265.
Balanus amphitrite var. *venustus;* Gruvel, 1903, 137.
Balanus amphitrite var. *venustus;* Annandale, 1906, 147.
Balanus amphitrite f. *venustus;* Broch, 1924*a*, 203, 204.
Balanus amphitrite venustus; Nilsson-Cantell, 1932*a*, 110.
Balanus amphitrite venustus; Nilsson-Cantell, 1938*a*, 37, text-fig. 8.
Balanus amphitrite venustus; Neu, 1939, 210.
Balanus amphitrite f. venustus; Gauld, 1957, 10.
Balanus venustus venustus; Harding, 1962, 283, pl. 6.
non Balanus amphitrite var. *venustus;* Gruvel, 1912, 346.
nec Balanus amphitrite venustus; Nilsson-Cantell, 1925, 28, pl. 1, fig. 3, text-fig. 11.
nec Balanus (s. str.) *amphitrite venustus;* Tarasov & Zevina, 1957, 189, text-fig. 74.

LOCALITIES: Ghana: (1–53) off Accra, Stas. 1, 2, 5, 6, 8–12, 14–17, 19, 21, 23, 27, 29–33, 53, 55–57, 59, 61–63, 67, 68, 70, 81, 83, 85–87, 93–96, 98, 99, 104, 106, 107, 121, 124–126, 129, 130; (54) Chorkor, Accra, in " bottom nets "; (55) Winneba; (56) off R. Densu; (57) Prince's Town; (58) Accra, 18–27 m., on *Turritella* sp. coll. R. Bassindale, B.M. 1953.2.5.2 (several spec.); (59) trawled off Accra, with *C. patula* on *Cymbium porcinum* pres. E. Salzen, B.M. 1957.6.3.1 (46 + 29 juv. spec.).

Nigeria: Lighthouse Beach, Lagos: (1) on cork cast up on beach, with *B. t. tintinnabulum* and *C. patula* (several dead spec.); (2) on a stone cast up on beach, with a Gorgonian (1 spec.).

To avoid excessive repetition in listing the records of this very abundant species the stations off Accra made by Mr. Bassindale have been cited above by number only. Fuller station details are given in Tebble (1955) and Bassindale (1961). Specimens have been collected from shells of the following Mollusca and Crustacea :

Gastropoda : *Turritella annulata* Kiener, *Solarium granulatum* Lam., *Crepidula porcellana* Lam., *C. porcellana* var. " Garnot " Adanson, *Natica collaria* Lam., *N. fulminea* Gmelin, *Murex hoplites* P. Fischer, *M. bourgeoisi* Tournouer, *Phos grateloupianus* Petit de la Saussaye, *Nassa tritoniformis* Kiener, *N.* cf. *plicatella* A. Adams, *Fusus boettgeri* v. Maltzan, *Olivancillaria* (*Agaronia*) *hiatula* Gmelin, *Cymbium porcinum* Lam., *Cancellaria cancellata* Linn., *Drillia rosacea* Reeve, *Clavatula muricata* Lam., *C.* (*Pusionella*) *nifat* Adanson, *Surcula coerulea* Weinkauft, *Turris pluteata* Reeve, *T.* (*Crassispina*) *carbonaria* Reeve, *Genota mitraeformis* Wood, *Terebra senegalensis* Lam. **Lamellibranchiata** : *Cardium costatum* Linn., *C. ringens* Gmelin, *Dosinia africana*, Gray. **Crustacea** : *Balanus tintinnabulum* var. *tintinnabulum* (Linn.), *Apiomithrax bocagei* (Osorio), *Calappa rubroguttata* Herklots.

The references in the literature to *B. amphitrite* var. *venustus*, Darwin by name are listed above. That they all refer to this variety is doubtful as discussed below. Weltner's record (1897) from Nagasaki was questioned by Nilsson-Cantell (1932*a*) presumably on account of its geographical separation from other records, as no morphological questions were raised.

There are only five illustrations of the variety in the literature. One, (Tarasov & Zevina, 1957) is a copy from Nilsson-Cantell (1925) which is not here considered to be var. *venustus*. There are thus only three valid illustrations ; of the whole shell (Darwin, 1854, pl. 5, fig. 2*a*), of a scutum and tergum (Nilsson-Cantell, 1938*a*, text-fig. 8) and of shell, opercular valves and appendages (Harding, 1962). Darwin's illustration of the hard parts of his varieties of *B. amphitrite* were not complete, which has undoubtedly led to some difficulty and misunderstanding of the varieties he proposed. Opercular valves of *venustus* are present in the Darwin collection of Cirripedia in the British Mudeum (Natural History) and these have been redescribed and figured by Harding (1962). The spur of the tergum is short and broad. This with the characteristic pink colour of the shell will in general distinguish the variety.

From the very extensive Ghanaian material it is possible to give an extended description of the variety. The shell is typically pink, sometimes bright but more often rather dull or " washed out ". Pale pink specimens also occur, but the shell is never red and only rarely approaches the purplish pink, of deeply coloured *B. pallidus*. Narrow vertical stripes of a deeper pink are present on the paries but may be absent or difficult to distinguish from the ground colour. Rarely the pink stripes are the only colour present (cf. some var. *stutsburi*). Shells with an orange tint occur rarely among normal pink ones.

From the many young specimens present it is evident that for some time after metamorphosis the shell of *B. venustus* is white. Pink pigment is developed quite suddenly as there is a rapid transition from white to pink shell. Young specimens thus have shells pink basally and with white summits to the compartments. The age, or size, at which pigment is first produced is very variable and a few never do so and remain pure white. When pigment is produced early in life, older specimens may be completely pink-shelled due to the disintegration of the tops of the compartments. Rarely, specimens occur with pigment on the margins of the paries only. When rather elongated these tend to resemble the *B. amphitrite* var. *pallidus* of Darwin. Such a specimen was found in the R. Densu collection listed above. It had a typical *B. venustus* tergum as here described.

The compartments are smooth or irregularly folded. Smooth specimens tend to be less heavily calcified and somewhat translucent so that the septate parietal canals are visible externally. The radii are moderately developed or narrow with very oblique summits when intact, white above and pink below. When intact the orifice is highly dentate. The epidermis is thin and not persistent. It bears horizontal rows of short fine hairs corresponding to the growth increments. Alae are well developed with less oblique summits than the radii. Internally the growth lines are prominent on alae and sheath. The sheath is overhanging, about one-third to one-half the length of the compartment. The compartments are prominently ribbed internally.

The scuta of three West African specimens are illustrated (Text-fig. 17*a*, *c*, *e*). The tergal and basal margins are of equal length, the basal angle being rounded off so that the slightly convex basal margin curves into the tergal. Growth lines are distinct but not prominent, the epidermis persistent in part and with hairs along the growth lines. The apex is acute when uneroded. There is a purple patch in the upper part of the valve but the apex is usually colourless. Rarely the whole scutum

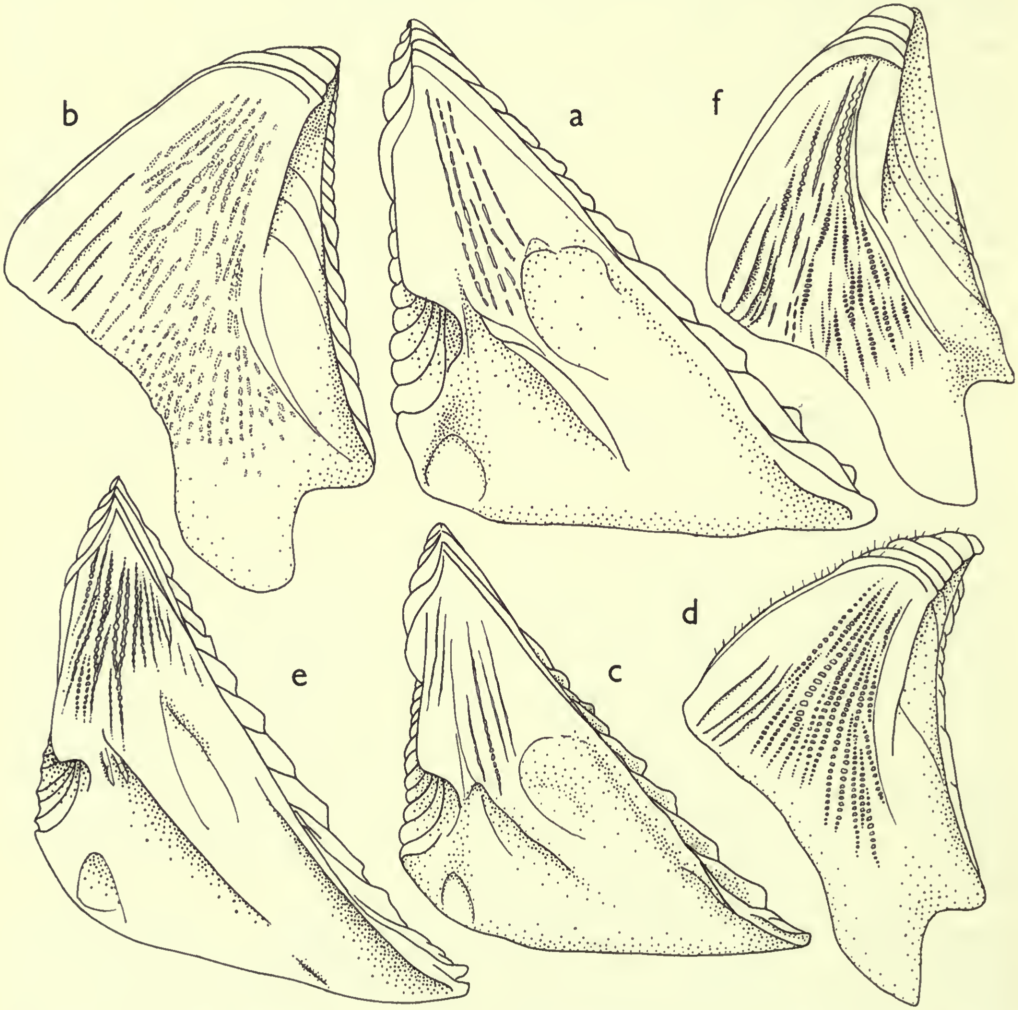


FIG. 17. *Balanus venustus venustus* Darwin. Internal views of the paired scutum and tergum of three specimens from off Accra : *a*, *b*, from Sta. 17 ; *c*, *d*, from sta. 31 ; *e*, *f*, from sta. 87 (*a*–*d* ×27 ; *e*, *f* ×14).

is colourless. There is no direct relationship between shell pigmentation and that of the opercular valves; of two shells with virtually identical pigment development, one may have a very small pale purple patch on the scutum and the other a deep purple patch covering the apical third of the valve. Very young colourless shells have colourless scuta. The outer surface is faintly striated from the apex. Internally the valve is thick with a prominent adductor ridge. The deep groove below the ridge and the deep depressor muscle pit between them delimit a raised area that in some specimens has the appearance of a low broad ridge. There is not a true second ridge. The adductor muscle pit is large and distinctly marked. The articular ridge is large, straight and reflexed over the articular groove. The inner surface of the valve is faintly striate in the area above the adductor ridge. The striations extend on to the articular ridge.

The terga corresponding to these scuta are illustrated in Text-fig. 17*b*, *d*, *f*. The valve is flat, triangular with a short broad spur about one third the width of the basal margin. Growth increments are marked by distinct grooves externally. The spur area also is demarcated by grooves only. The articular margin is slightly concave, the carinal margin convex, the basal margin on the carinal side straight or more usually slightly concave. Internally the articular ridge is long but not very prominent, the articular groove long and deep. Crests for the depressor muscle are only feebly developed and about four in number. The internal surface is more or less striated longitudinally, the striations being finely tuberculated.

The above descriptions of scutum and tergum are in close agreement with the figures given by Harding (1962, pl. 6, figs. *d*–*g*) for the lectotype of *B. venustus venustus*.

Opercular valves of "*venustus*" have been figured by Nilsson-Cantell (1925, 1938*a*), the two figures representing very differently shaped valves. The Indian specimens (Nilsson-Cantell, 1938*a*), have valves similar to those shown here though there are some differences. Thus the scutum has a basi-tergal angle of $< 90°$ and the corner of the valve is not rounded off: also, the articular ridge projects a little in front of the valve margin. The tergum is more angularly triangular mainly due to the very straight carinal margin. In other respects these valves appear to agree reasonably with the West African *venustus*.

The variety figured by Nilsson-Cantell (1925) has very different valves. The tergum has a long narrow spur and many crests for the depressor muscles. The shell is said to be red (" rot ") and the colour to agree best with that of *venustus*. But no *venustus* in the present collection from West Africa is red. The statement that the stripes are not confluent—a character attributed to *stutsburi*—is not valid as *stutsburi* has often clear distinct stripes. In the scutum the depressor muscle pit is said to be indistinct (" unbedeutend "), which is not the case for *venustus* as here considered. It is considered that the specimens are referable to Darwin's var. *Stutsburi*, i.e. *B. pallidus* Darwin of this work.

Excluding the rejected figures given by Nilsson-Cantell (1925) and copied by Tarasov & Zevina (1957) there were no illustrations or valid descriptions of the appendages of *B. venustus* until Harding (1962) published photographs of a lectotype from Natal. The mouth-parts of a specimen from Accra are described and figured here. The labrum (Text-fig. 18*a*) has the two halves of the margin set at an angle so that the median toothed area is prominent. There are two or three teeth on either side of the wide V-shaped notch. Sparse short hairs are present round the teeth and in the upper part of the notch. Hairs are absent in Harding's photograph (1962, pl. 6*c*). The palp (Text-fig. 18*b*) is rectangular, tapering slightly towards the rounded extremity. The anterior margin is slightly concave, the posterior convex. The hairs on the concave margin are short. A band of similar short hairs on the inner face of the palp merges into the long hairs of the extremity. A row of long hairs begins on the face, runs to the posterior margin of the palp and follows this margin to merge with the apical hairs.

The mandible (Text-fig. 18*c*) has five teeth, the third to fifth lying close together. The first is normally simple but occasionally bifid at the tip. The second is simple or with a small cusp which when close to the tip renders this bifid. The third to fifth teeth are usually blunt from use but in the developing cuticle are sharp. The third tooth has one or two secondary cusps but occasionally may be simple. The

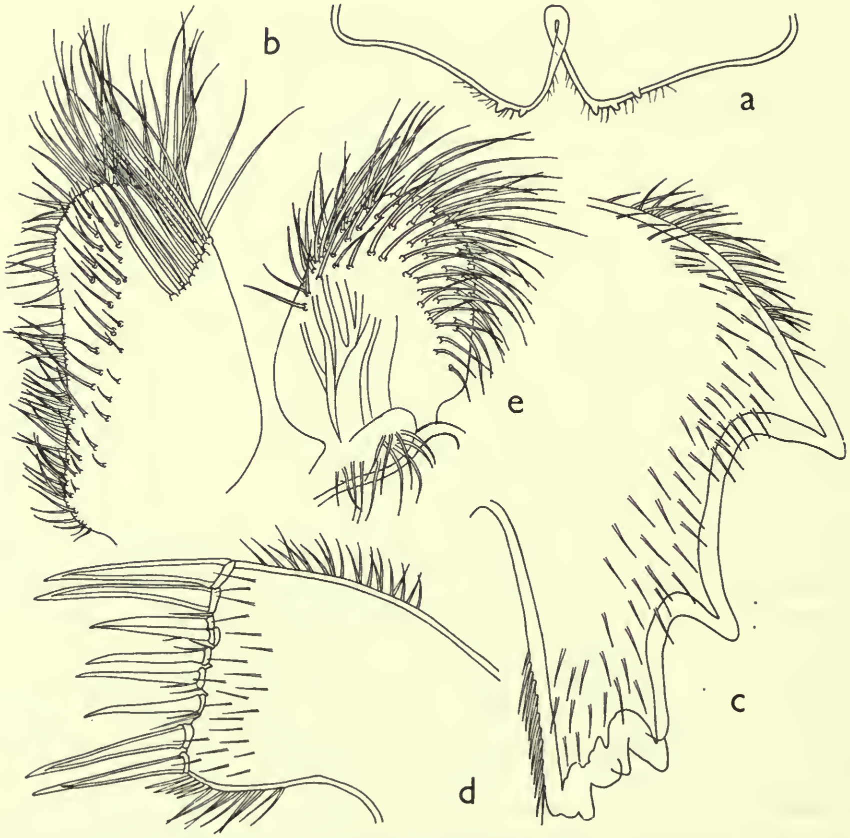


Fig. 18. *Balanus venustus venustus* Darwin. Mouth parts of a specimen from Sta. 87 off Accra. *a*, labrum (×58) ; *b*, palp (×45) ; *c*, mandible ; *d*, maxilla I (both ×100) ; *e*, maxilla II (×45).

fourth is double with two sharp equal points when new but usually worn down in use. The fifth is very close to the lower angle and when worn apparently confluent with it. In the developing cuticle it is distinct and there are two sharp stout spines below it on the lower angle. Harding's illustration (pl. 6*n*) would appear to be of a worn mandible as the lower angle is blunted.

Maxilla I (Text-fig. 18*d*) has a straight biting edge. The lower pair of spines is about as large and stout as the upper pair. There are five intermediate spines, though occasionally four or even only three. There is a small tuft of short stout hairs or fine spines on the lower angle. Of six pairs of maxillae examined, in two there was a difference in number of intermediate spines in the left and right maxilla.

Maxilla II (Text-fig. 18*e*) is broadly oval tapering slightly to the tip, which is densely clothed with long fine setae. There is a very small lower lobe.

Cypris larvae were present on some mollusc shells. Two from a valve of *Cardium ringens* measured

0·75 mm. long × 0·31 mm. high × 0·27 mm. broad
0·73 × 0·30 × 0·26

and a third unattached specimen was 0·676 mm. long.

The present material comes entirely from below low-tide level. According to Buchanan (1958) *B. venustus* is a common member of the sessile epifauna of the " inshore fine sand " and " sandy silt " communities off Accra, i.e. from 3–20 fathoms (5·5–36·5 m.) depth. The present collections show it to be abundant from 10–20 m. and rather less common from 20–25 m., that is over the deeper part of the fine sand community and the shallow part of the sandy silt community. Here it is abundant on shells of *Cardium ringens* Brug. and especially *Turritella annulata* Kiener, both living and dead. As many as 74 specimens, all but three alive, were found on a single *Turritella* shell. It is by no means confined to these molluscs as the extensive list above testifies. The two records of material cast on shore at Lagos suggest that *venustus* occupies a similar habitat there. Shallow water dredgings in the Bonny estuary, Eastern Nigeria, failed to obtain this variety. Records from the " Atlantide " and " Calypso " Gulf of Guinea expeditions (Stubbings, 1961*a*, *b*) indicate that *B. venustus* is distributed from Gambia to the R. Congo. The fact that most specimens from the latter locality came from 25 m., or deeper and were dead, suggests that the normal habitat of *B. venustus* is in the 10–20 m. depth zone.

A number of specimens from Accra Sta. 2 were attached in the grooves on the convex side of *Cardium ringens* valves. All were orientated along the grooves and elongated along the rostro-carinal axis, with the carinal end directed towards the highest part of the shell. Thus the few barnacles in the shallower part of the grooves near the umbo were orientated at 180° to the majority in the deeper furrows nearer the shell lip.

B. venustus was not obtained from the intertidal zone by either of the above expeditions, nor by Bassindale or the author. Neither was it found on mangrove roots, a common habitat of estuarine species in West Africa. It is evidently confined to the open sea. This is of significance in that it supports the view that the form found by Gruvel (1912) on mangroves in the lagoon at Grand Bassam, Ivory Coast, and that reported by Nilsson-Cantell (1925) on mangroves from the Cameroons, are not *venustus*. The mangrove fringed estuarine creeks of tropical West Africa are the habitat of *B. pallidus* Darwin.

B. venustus appears to be very widely distributed in tropical waters. Whereas now it is perhaps best known from West Africa it is also found in S. Africa (Darwin), Ceylon (Annandale, 1906) India (Nilsson-Cantell, 1938*a*). Weltner's record from Nagasaki (Japan) has already been noted as doubtful (Nilsson-Cantell, 1932*a*). That it has not been recorded by Hiro (Utinomi) from Japan confirms this doubt. This absence from the literature on Far Eastern barnacles casts further doubt on the record by Tarasov & Zevina (1957).

Balanus venustus niveus Darwin

Balanus venustus niveus: Harding, 1962, 286, pl. 7, figs. *a–r*.
Balanus venustus niveus: Stubbings, 1964*b*, 340.

A number of more or less translucent white "*B. amphitrite*" from the Sierra Leone river, Port Harcourt and Bonny, Nigeria, were at first assigned to this variety. A further examination cast doubts upon this determination. In the first place all the specimens were associated with more or less pigmented *B. pallidus*. A more detailed examination after removal of epizoic growth and debris from the compartments and opercular valves showed that an appreciable number had slight traces of pinkish-purple pigment, either as small streaks or spots on the body of the paries or as small marginal lines. Patches of pigment were present also on the scuta, though smaller than on well-pigmented individuals. As no pigment is recorded for the Darwin type of var. *niveus*, it seemed probable that these specimens were really very poorly coloured *pallidus*.

In typical specimens, of course, the tergum of *pallidus* is very distinctive having a long spur and much emarginated basal margin whereas that of *niveus* is short and broad and obliquely truncated In the terga of the specimens in question the spur is not typical of either form, being shorter than in *pallidus* but less broad in proportion than in *niveus*. They could be regarded as rather atypical specimens of either variety. As, however, pigmented specimens in the same collections had similar terga it is considered that the whole sample in each case belonged to one variety and the material is all regarded as *B. pallidus*.

There is not, therefore, any material in the collections under review that can be assigned with certainty to *B. venustus niveus*. In all the West African collections examined by the author with one exception, *B. v. niveus* has been absent. In material from the Congo estuary (Stubbings, 1964*b*) a few specimens were found which appeared to belong to this variety. As concluded in that report, *B. v. niveus* is very rare in West African waters and may well occur sporadically as a shipborne immigrant.

The above record from the R. Congo is the only one from the eastern Atlantic though Kolosvary (1951) cites the Mediterranean and Darwin (1854) South Africa. Neither record has been confirmed. Further afield there are a number of scattered records of *niveus* from the Indian Ocean and the Malay Peninsula. As the variety is common on the American shores from Massachusetts to Southern Brazil and according to Kolosvary (1943*a*) occurs at Montevideo, Uruguay and even in Tierra del Fuego, there is ample scope for shipborne transport of this variety as with other forms of "*B. amphitrite*" and some at least of these scattered records may represent such local introductions.

Balanus fallax Broch

Balanus (*Hesperibalanus*) *fallax* Broch, 1927, 26, pl. 2, figs. 12–17 ; pl. 3, figs. 18, 19 ; text-figs. VII–IX.
Balanus (*Hesperibalanus*) *fallax:* Utinomi, 1959*b*, 402, text-fig. 1.
Balanus occidentalis Stubbings, 1961*a*, 34, text-figs. 8–11 ; 1961*b*, 189.
Balanus fallax: Stubbings, 1963, 30, text-figs. 10, 11.

LOCALITIES: Ghana: Accra, (1) Sta. 133, 51 m. (1 spec.); (2) 14 m., in sponge, 27.4.51 (1 spec.); (3) Osu Fisheries Sta., 19.5.51 (4 spec.); (4) near R. Densu, 15 miles from Accra, 16.5.51 (1 spec.).

The above material has been compared with the original material designated as "types" by Professor Broch. The shell and appendages have been redescribed in some detail (Stubbings, 1963) and it is only necessary here to comment on points of interest in the Ghanaian material.

The specimens exhibit in general a more strongly developed shell. That from 14 m. in a sponge is mottled pink like the type material but the others have regular lines of pigment except towards the margins of the compartments where the lines are broken up into blotches or spots of a deep pink colour. None of the specimens shows longitudinal striations on the scuta.

The internal sculpturing of the scuta is strongly developed (Text-fig. 19*a*, *c*, *e*). The adductor scar is a distinct pit deepest on its apical border. There is no adductor ridge but the valve is appreciably thickened below the adductor pit. In the specimen from the R. Densu (Text-fig. 19*e*) there is a faint suggestion of a short ridge parallel to the basal margin immediately below the adductor pit. The pit for the lateral depressor muscle is more marked in these somewhat heavier valves. The basitergal angle according to Broch (1927*a*, figs. 16, 19) and Stubbings (1963, fig. 10) is 90° or more. In one specimen (Text-fig. 19*c*) this angle is less than 90° though in another specimen (Text-fig. 19*e*) the angle is distinctly obtuse.

A point not brought out in Broch's figures is the scroll-like form of the upper part of the articular ridge of the scutum. This is well marked in the specimens here illustrated. The degree of development of this scroll affects the shape of the lower end of the articular ridge. If the scroll is weak, as in Broch's illustration and Text-fig. 19*e*, then the ridge ends abruptly. But when the scroll is strongly marked (Text-fig. 19*a*, *c*) then it extends to the lower part of the articular ridge and the ridge ends less abruptly, curving into the plane of the valve.

Terga from two barnacles from Osu are shown in Text-fig. 19*b*, *d*. The chief points of interest are the presence of fine hairs on the epidermis of the growth ridges, the broad spur and the strongly developed crests for the depressor muscles. There is a distinct tendency for small incipient crests to develop near the base of the spur. The specimen from near the R. Densu (Text-fig. 19*f*, *g*) has a less robust tergum.

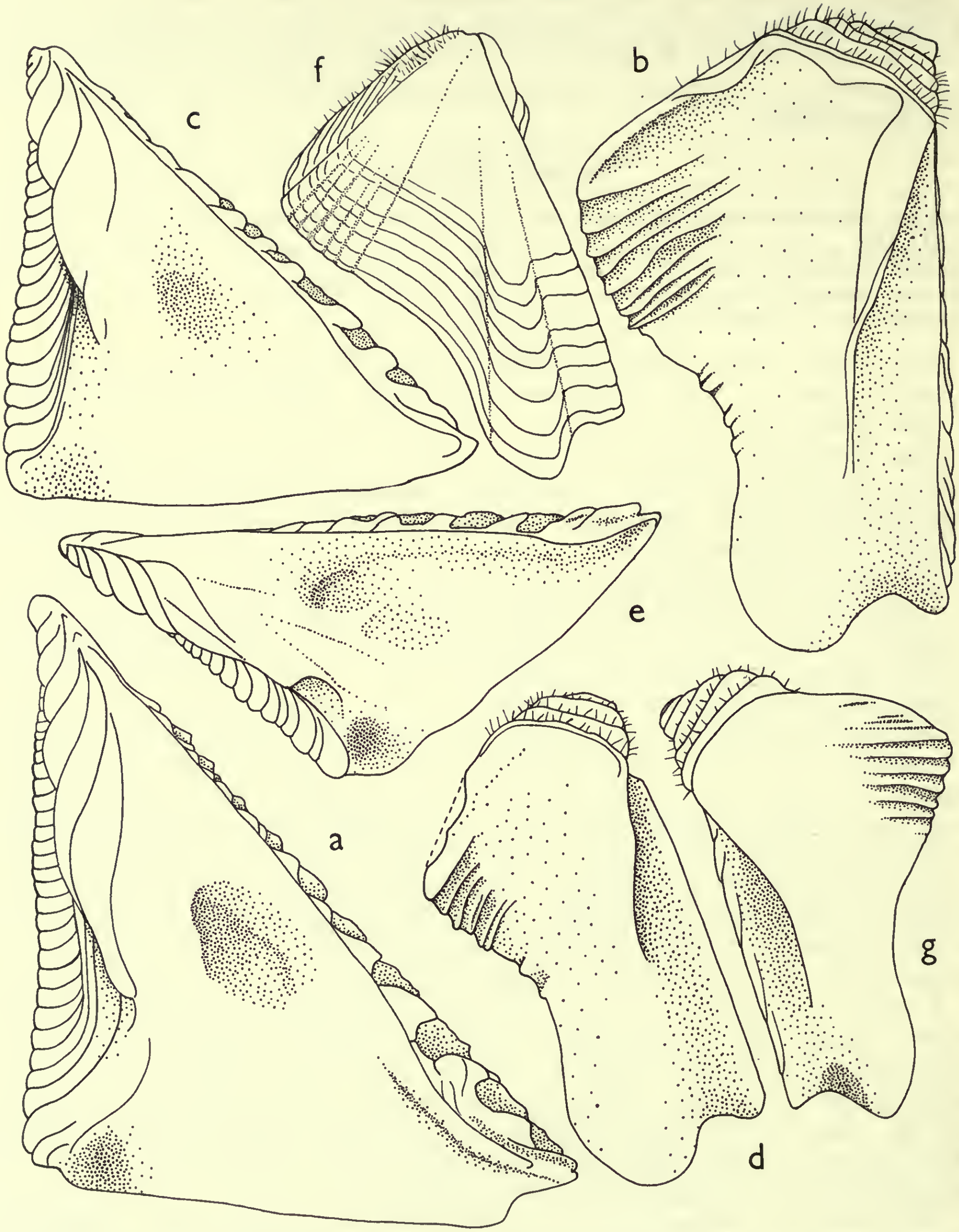


FIG. 19. *Balanus fallax* Broch. *a*, *b*, internal views of scutum and tergum of a specimen from the Osu Fisheries Station, Accra, Ghana ; *c*, *d*, similar views of valves of another specimen from Osu : *e*, *f*, *g*, internal view of scutum and external and internal views of a tergum of a specimen from the R. Densu, Ghana (all ×28).

The spur is much narrower and is pointed at its extremity instead of being rounded as in the heavier Osu specimens. There are no incipient crests in the concave basal margin of the valve. In both these points it agrees with the specimen figured by Utinomi (1959*b*).

Illustrations of the mouth appendages have been given by Broch (1927*a*) and Stubbings (1961*a*, 1963). A few notes on minor variations may be given. The teeth on either side of the labrum (Text-fig. 20*a*) may be directed obliquely away from the mid-line instead of standing perpendicular to the border of the labrum. The palp (Text-fig. 20*b*) agrees with that figured by Stubbings (1961*a*). It is oval or somewhat rectangular, the anterior margin being almost straight, the posterior and distal margins curved. There is a double row of pectinate setae along the anterior margin. The mandible (Text-fig. 20*c*) has been fully described previously. The third and fourth teeth are somewhat bifid and the lower angle has 3 more or less complex teeth, sharply pointed in some specimens but blunt in others. This is probably a matter of wear only. The setae on the lower margin may be described as stout. Whether they should be regarded as " spines " depends on the degree of individual development and a somewhat arbitrary interpretation of the point where a stout seta becomes a spine. The setae on the R. Densu mandible figured were appreciably stouter than those on an Osu specimen. The first maxilla of the Osu specimen (Text-fig. 20*d*) had the small spine lateral to the two large upper spines, as described by Broch. In the R. Densu specimen this spine was absent. The second maxilla is oval and tapers distally to a rounded point. The lower lobe is semicircular. In the R. Densu specimen the second maxilla was much narrower than in the Osu specimens.

The segmentation of the cirri was given by Broch (1927*a*) and in a paratype by Stubbings (1963). The number of segments in cirri I and VI was appreciably lower in the paratype. The segmentation in the cirri of the paratype agreed closely with that of *B. occidentalis* (= *B. fallax*) in Stubbings (1961*a*). Three new counts of segments are now available (Table 6). They agree substantially with earlier counts. It may be noted that in the Accra specimen the number of segments in cirrus VI equalled that given by Broch. In no specimen so far examined has there been 15 segments in the anterior ramus of cirrus I as described by Broch.

TABLE 6

Specimen	I	II	III	IV	V	VI
Accra, 14 m.	12·9	9·7	11·10	18·18	21·22	22·22
R. Densu	13·7	10·10	10·9	18·14*	17·23	17·18
Osu	11·7	9·8	9·8	11*·14*	19·18	20·21
Mean	12·7	9·8	10·8	17·17	19·21	19·20

TABLE 6. Number of segments in the cirri of three specimens of *B. fallax* Broch from three localities in Ghana. * tip of cirrus missing.

The presence of a dorsal process at the base of the penis (Stubbings, 1963) has been confirmed. It is sharply conical, slightly curved and bears a single long seta (Text-fig. 20*f*).

B. fallax is known only from the African coast, from Algiers in the Western

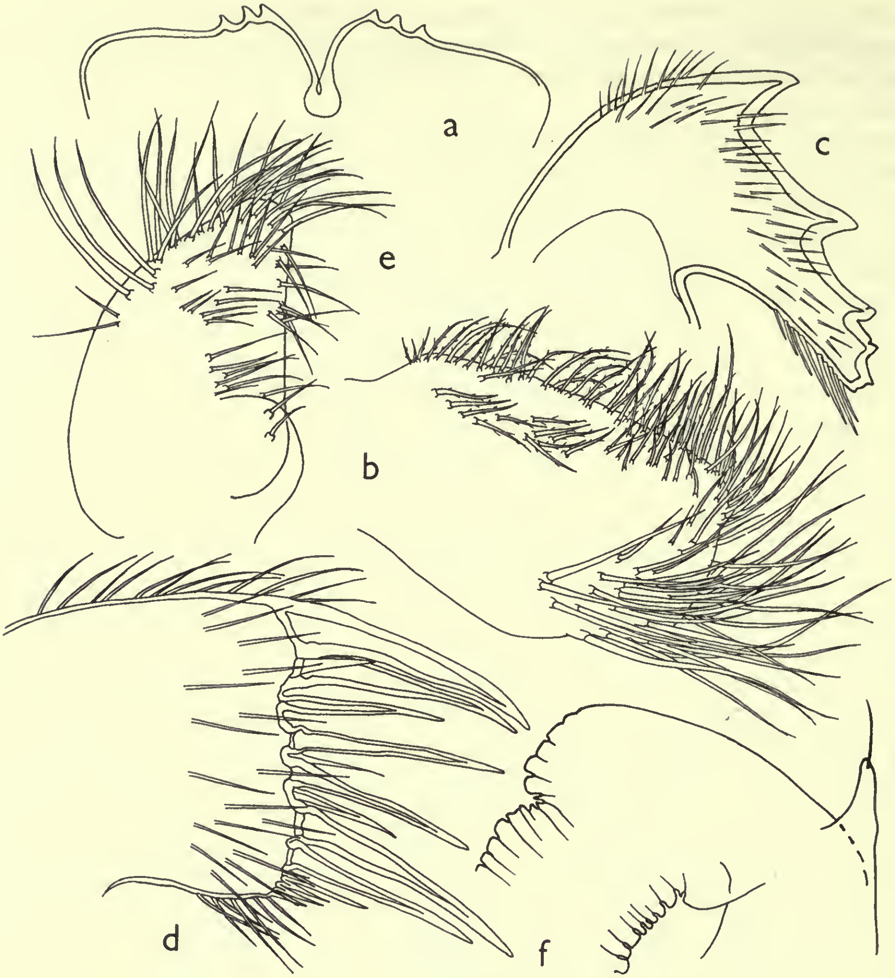


FIG. 20. *Balanus fallax* Broch *a*, labrum ; *b*, palp ; *c*, mandible ; *d*, maxilla I ; *e*, maxilla II ; *f*, base of penis with dorsal spine (*a–c*, *e*, *f*, ×95 ; *d* ×180).

Mediterranean, down the west coast as far as Cape Ledo in Angola. Where more intensive collecting has been done, e.g. Morocco, French Guinea and Angola, there are a number of records, suggesting that the species is common. But there are few specimens in the Ghana collections and none at all from the Gulf of Guinea, suggesting that *B. fallax* is not uniformly distributed over the West African coastline.

Balanus (Conopea) calceolus Darwin

LOCALITIES: Ghana: Accra, (1) Chorkor, on the horny stem of an alcyonarian, –.3.49 (2 dead and without opercular valves); (2) Chorkor, on a violet and yellow alcyonarian and other alcyonarians, 1.2.50 (11 + 13 dead spec.); (3) Chorkor, on the same violet and yellow alcyonarian, 12.5.50 (1 spec.); (4) Christiansborg shore, on the same alcyonarian sp., 19.11.49 (4 + 3 juv. spec.); (5) 10 miles off-shore, on a white alcyonarian, 8.5.49 (3 + 1 dead spec.); (6) off Accra, on the violet and yellow alcyonarian, 13.11.51 (1 spec.); (7) 15 m. from Accra beyond Densu 16.5.51 (6 spec.).

Specimens from locality (7) above contained developing eggs of average size 222 × 109 μ.

B. calceolus is known from the Mediterranean and the Atlantic off the Straits of Gibraltar (Darwin, 1854; Caziot, 1921; Utinomi, 1959*b*). On the West coast of Africa it is recorded from Rabat, Morocco (Broch, 1927*a*), Cap Blanc, Mauretania (Broch, 1924*b*), Sierra Leone (Nilsson-Cantell, 1928), Ghana (Gauld, 1957), the Congo and Angola (Nilsson-Cantell, 1938*b*: Stubbings, 1963, 1964*b*). From South Africa Stebbing (1910) records it from Bird Island, Algoa Bay.

B. calceolus has therefore been found at localities spaced along the whole west coast of Africa. There are some considerable gaps between known localities. It is surprising that there are no specimens in the collections of the IFAN, Dakar, in view of the extensive collecting done by that Institution. The absence of records in the Gulf of Guinea may be due to less intensive collecting, or may represent a discontinuity in distribution clearly seen for several other species.

Proceeding eastward it is known from Wasin, E. Africa (Gruvel, 1907*a*), Madras (Darwin, 1854; Nilsson-Cantell, 1938*a*), the E. Indies (Broch, 1922, 1931; Pilsbry, 1916), Japan (Weltner, 1897; Hiro, 1937; Utinomi, 1949, 1958) and from Western Australia (Weltner, 1897).

B. calceolus has therefore an "old world" distribution in warm to tropical seas, extending from the eastern Atlantic eastward to the Indian Ocean and the seas bordering S.E. Asia. It has not been recorded from the remainder of the Pacific and is unknown from the western Atlantic Ocean.

TETRACLITA Schumacher

Very few specimens of *Tetraclita* have been collected in West Africa and the several groups have been assigned to different species by the respective authors. Pilsbry (1916) and Gauld (1957) each record one species from the coast. I disagree with Gauld as to some of his material and consider it belongs to a third species *T. divisa* Nilsson-Cantell (1921). It is questionable whether there are indeed three species in the area but much more material is required from the old collecting sites and elsewhere before an authoritative pronouncement can be made as to how many and which species occur there. The three species in question are discussed below.

Tetraclita divisa Nilsson-Cantell 1921

Tetraclita divisa Nilsson-Cantell, 1921, 362, pl. 3,* fig. 11, text-fig. 83.
Tetraclita divisa: Hiro, 1939, 275, text-fig. 15.

LOCALITY: Ghana: Hospital Reef, Axim, 13.4.49 (2 spec. one without soft parts or opercular valves).

This species is closely related to *T. purpurascens* (Wood) with which it agrees in having a transversely elongated scutum. Whereas *T. purpurascens* has the spur of the tergum united with the basiscutal angle and the valve elongated, *T. divisa* has a triangular tergum with distinct short and broad spur, separated from the basiscutal angle by about half its width (Text-fig. 21*a*).

Nilsson-Cantell (1921) states that the scutum has no adductor ridge or crests for depressor muscles, but Hiro (1939) finds the adductor ridge may or may not be present and figures (1939, fig. 14*B*) a scutum with a ridge. Zevina & Tarasov (1963) state that the ridge is little developed and do not show it in their figure. The present complete specimen has an adductor ridge (Text-fig. 21*b*). There are no crests for the lateral depressor muscles but a series of about 6 shallow pits for the muscle insertions.

The compartments have well developed radii with horizontal summits. In both specimens the walls are worn, in one so much so that only faint traces of the radii remain. The growth lines on uneroded compartments are fringed with hairs. There are up to six rows of pores in the paries, rather more than described by Hiro. No

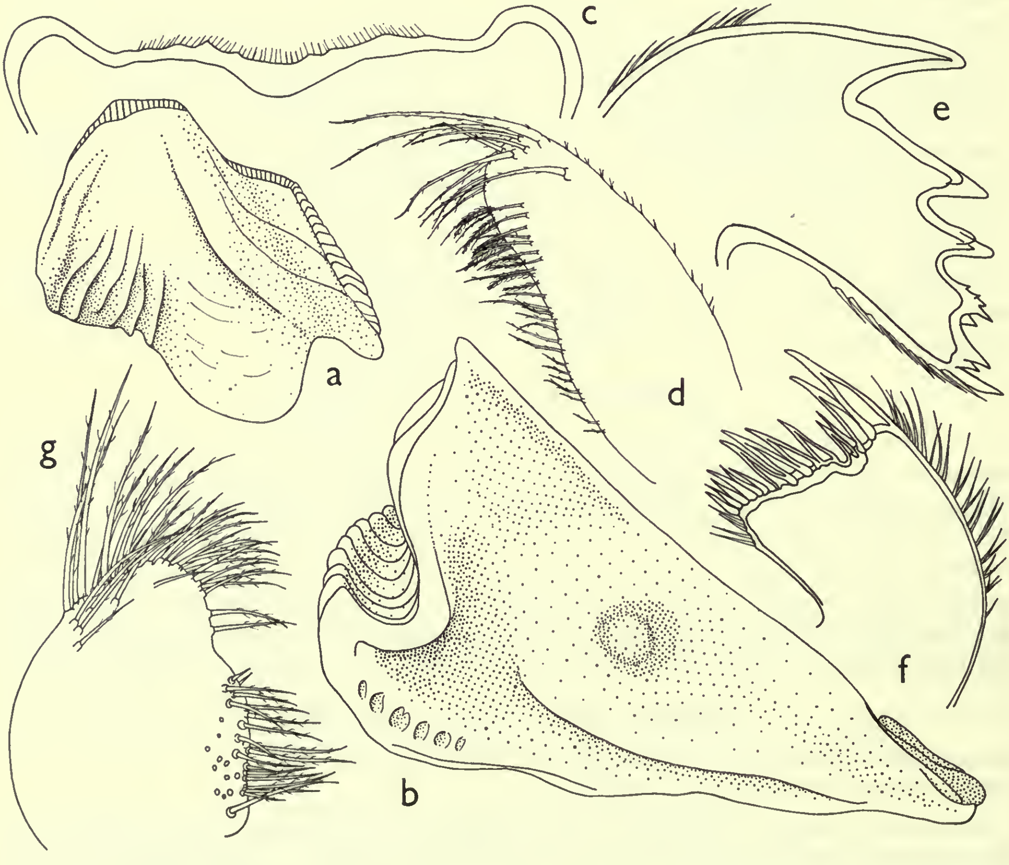


FIG. 21. *Tetraclita divisa* Nilsson-Cantell. *a*, internal view of tergum, *b*, of scutum (both ×40); *c*, labrum, *d*, palp, *e*, mandible, *f*, maxilla I, *g*, maxilla II (*c*, *e–g*, ×160; *d*, ×120).

trace of basis remains in one specimen. In the other there are fragmentary remains of a rather thin calcareous basis near the walls. The central area of the basis is wanting. Hiro states that the basis in *T. divisa* is calcified peripherally only.

The mouth parts agree substantially with the description of the species by the above authors. The labrum (Text-fig. 21*c*) is even more weakly bowed than in Nilsson-Cantell's figure, being almost straight from side to side with minor irregularities. There are three or four slight prominences, scarcely teeth, on either side of the middle line, as against only two in Hiro's specimen. The palp (Text-fig. 21*d*) is very similar to Nilsson-Cantell's figure even to the rather brushlike plumose setae on the anterior edge. The mandible (Text-fig. 21*e*) has a subsidiary cusp or cusps on all but the first tooth as in Nilsson-Cantell's and Zevina & Tarasov's figures. The fourth tooth has several sharp-pointed cusps as figured by the above authors. Maxilla I (Text-fig. 21*f*) agrees very closely with those figured by Hiro and Nilsson-Cantell. There are minor differences in the arrangement of the central spines relative to the notch in Zevina & Tarasov's figure. Maxilla II (Text-fig. 21*g*) has been figured by Zevina & Tarasov (1963), who show no plumose setae. Plumose setae in the present specimen are restricted to a group at the tip of the appendage and to a second group on the rather protuberant lower part of the anterior border.

The number of segments in the cirri is given in Table 7.

TABLE 7

	I	II	III	IV	V	VI
Ghana	10·5	6·5	5·5	11·11	12·13	14·14
Nilsson-Cantell	8·4	6·5	6·5	12·12	12·12	12·12
Hiro	10·6	8·7	7·6	11·12	14·14	14·14
Zevina and Tarasov	8·5	6·6	6·4	–·8	8·7	9·8
	—	6·5	6·4	7·6	11·9	10·9

TABLE 7. Comparison of number of segments in the cirri of a specimen of *T. divisa* from Ghana with the number given by Nilsson-Cantell (1921), Hiro (1939) and Zevina & Tarasov (1963).

There is close agreement between the number of segments given by the earlier authors and that found in the present specimen. The figures quoted by Zevina & Tarasov (1963) for cirri IV to VI are appreciably lower.

T. divisa was originally described (Nilsson-Cantell, 1921) from Sumatra and Java from material collected by C. W. A. Aurivillius. The only subsequent records are by Hiro (1939) from the east coast of Formosa and by Zevina & Tarasov (1963) from the South China Sea. Its occurrence on the west coast of Africa extends enormously the known distribution of this species and suggests a probable distribution over much of the tropics of the Old World, as it is unlikely this will prove to be an isolated occurrence.

Tetraclita purpurascens Wood

T. purpurascens is included here on the authority of Gauld (1957) who recorded specimens from Victoria, Cameroon and Axim, Ghana. There are no other records of this species from West Africa. It is stated that the specimens corresponded

" exactly " with Darwin's (1954) description. Dr. Gauld informs me (in litt.) that this statement referred specifically to a group of specimens from Victoria and might not be true for the material from Axim. It is possible that this Axim material was originally part of that here described as *T. divisa* Nilsson-Cantell. Unfortunately the Victoria material is no longer available for re-examination.

Tetraclita squamosa squamosa (Bruguière)

Tetraclita squamosa squamosa: Pilsbry, 1916, 251.

Pilsbry (1916, 252) cited two groups of specimens from " West Africa " and " Cape Palmas " (Liberia) which he assigned to the typical subspecies of *T. squamosa* at the same time noting certain differences. It has not been recorded subsequently from West Africa.

PYRGOMA Leach 1817

Pyrgoma anglicum G. B. Sowerby

LOCALITIES: Ghana: (1–5) Accra: (1) Sta. 45, 35 m., on dead coral (1 spec.); (2) Sta. 131, 37 m., attached on or near base of the living solitary coral *Balanophyllia formosa* Gravier, 2.5.51 (5 + 1 dead spec.); (3) Sta. 133, 51 m., on a single dead solitary coral (6 dead spec., also remains of the bases of 12 others); (4) no locality, on *Oculina* (*Schizoculina*) *fissipora* Milne-Edwards & Haine received from Dr. D. T. Gauld, University of Ghana (4 dead spec.); (5) on *Caryophyllia* sp. –.2.55, coll. J. B. Buchanan (7 spec.); (6) Axim. " from coral *Astrangia* sp. " –.6.55, coll. J. B. Buchanan (3 spec. without basis or soft parts).

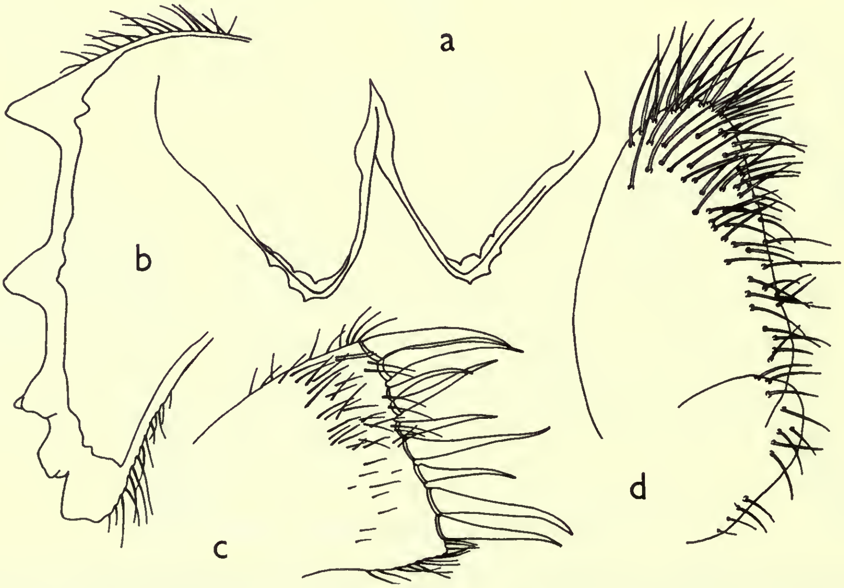


FIG. 22. *Pyrgoma anglicum* Sowerby from Accra. *a*, labrum (×83), *b*, mandible, *c*, maxilla I, *d*, maxilla II (all ×135).

Nigeria: Bonny River Estuary, off Bonny, from a coral dredged in shallow water, 28.1.58 (21 + 3 dead spec.) (H.G.S.).

Dr. Buchanan states (in litt.) that he collected *Pyrgoma* in 1954 from 20 m. off Takoradi, Ghana on *Oculina* sp. and in 1955 from the shore at Dixcove, Ghana on *Porites* sp. and *Siderastrea radians*.

Illustrations of some of the appendages have been given by Broch (1927*a*). The labrum is of the high conical form described by Broch but has three distinct teeth, not one, on either side (Text-fig. 22*a*), thus agreeing with Darwin's description of the labrum of this species. The outermost of the three labral teeth is smaller than the other two. The palp is oval and of the typical form. The mandible (Text-fig. 22*b*) has a rather straight edge, the teeth being rather broad and blunt. The third tooth is slightly bifid. In Broch's specimen the second tooth was slightly bifid. The lower angle is composed of two blunt rounded teeth. There are very few hairs on the surface of the appendage. The first maxilla (Text-fig. 22*c*) agrees closely with that figured by Broch. The edge is straight and without a notch. The large upper spine is followed by eight others of which the first, fifth and last two are rather larger than the others. The surfaces of the appendage are hairy. The second maxilla (Text-fig. 22*d*) is narrowly oval with a small oval lower lobe. It is densely setose along the inner margin and apically. The segmentation of the cirri is shown in Table 8, agreeing reasonably well with that given by Broch (1927*a*):

TABLE 8

	I	II	III	IV	V	VI
Accra	16·9	7·9	8·9	15·16	18·18	19·19
Broch	17·8	7·9	8·10	17·19	18·22	20·23

TABLE 8. Number of segments in the cirri of a specimen of *P. anglicum* from Accra, compared with Broch's (1927) figures.

The segments of the inner ramus of cirrus I are moderately protuberant, those of the outer ramus scarcely so. Cirrus II is very small. Hooked spines occur on segments 2–6 of the inner ramus of cirrus III. Cirri IV–VI have rather fewer segments than in Broch's specimen. In cirrus IV the first four segments are distinguishable though probably fused. The number of hooked spines on each segment of the inner ramus of cirrus IV, compared with the number given by Broch (1927*a*), is shown in Table 9.

TABLE 9

Segment	1	2	3	4	5	6	7	8	9	10
Accra	1	2	2	2	2	2	2	1+r	1	0
Broch	1	2	2	1	2	2	2	2	1	r

fused segments

r = rudimentary spine

TABLE 9. Number of hooked spines on the lower segments of the inner ramus of cirrus IV in *P. anglicum*.

The penis is long and closely annulated and has a basidorsal point.

The coral host of the Bonny specimens eventually grows over the barnacle and entombs it. From the nodular form of the coral specimen and the fact that several nodules revealed enclosed *Pyrgoma* when broken open it is possible that many *Pyrgoma* are so buried. Scuta and terga are present in many of these buried shells so overgrowth of the coral presumably occurs whilst the barnacle is still alive.

Rees (1962, 1966) has discussed the distribution of *P. anglicum* with particular reference to its coincidence with that of the solitary coral *Caryophyllia smithii* in British waters. Rees also indicates the wider distribution of the species southwards to Spain, the Mediterranean and West Africa. To Rees's references may be added Sicily (Kolosvary, 1951) and the Cape Verde Archipelago (St. Iago and Brava) (Stubbings, 1963). These localities confirm Darwin's (1854) earlier records. Gauld (1957) cites *Astrangia* and *Caryophyllia* as host corals off Accra, Ghana, but these coral identifications need confirmation. Gruvel (1903), not quoted by Rees, reported specimens in the Paris Museum from Algeria on *Coenocyathus anthophyllites* and others from " Travailleur " St. 34 on *Dendrophyllia cornigera*, the same host as recorded by Broch (1927*a*) from the coast of Morocco. The present records from Bonny, E. Nigeria represent the furthest kown southerly limit of the species in the Eastern Atlantic.

The Far Eastern records cited by Rees may be extended by adding Madras (Nilsson-Cantell, 1938*a*) and Seto, Japan (Hiro, 1937). Hiro (1935) also apparently accepts Broch's (1931) record of " *Pyrgoma* sp. aff. *anglicum* " from Sagami Bay, Japan as a true *P. anglicum*.

CHELONIBIA Leach 1817

Four species of *Chelonibia* have been recorded from West Africa.

Chelonibia testudinaria (Linnaeus)

LOCALITIES : Senegal : from scutes of a turtle, coll. Captain Moloney, B.M. 85.5 (5 large and 2 very small spec.).

Ghana, Accra, 8, pres. Dr. D. T. Gauld (no further data).

The Ghanaian specimens range in size up to 30 mm. carino-rostral diameter. All the shells are disarticulated and the soft parts wanting. The " teeth " on the radii are poorly developed or wanting in these small specimens.

The species is found in Ghana on turtles coming ashore on the sandy beaches and killed by the villagers, but few specimens seem to have been collected. It has been recorded previously from " equatorial Africa " (Gruvel, 1905), Cameroons (Nilsson-Cantell, 1921), Ghana (Gauld, 1957) and Senegal (Stubbings, 1965). It has not been recorded from the more temperate waters of north-west Africa. A number of records for the Mediterranean including the Adriatic are summarized by Kolosvary (1943*a*, 1951). Barnard (1924) records it from Table Bay, South Africa.

Further afield *C. testudinaria* is generally distributed throughout the tropical and warmer temperate seas.

Chelonibia caretta (Spengler)

Records of this species on the West African coast are few and widespread. Darwin (1854) recorded it from the " West Coast of Africa " without further indication of locality. Broch (1924*b*) described it from the Baie du Levrier, Mauretania and in the same year Barnard (1924) from Table Bay, South Africa. Pilsbry (1916) also mentions specimens from the Cape of Good Hope. There appears to be no other record from the west coast of Africa. It is not represented in any of the recent expedition collections. Neither is it present in the collections of the Institut Français d'Afrique Noire. We may conclude, therefore, that *C. caretta* is rare on the west coast of Africa.

Chelonibia manati Gruvel

Chelonibia manati Gruvel, 1903, 116, pl. 2, figs. 14, 17, 18; pl. 4, figs. 15, 16.
Chelonibia manati: Stubbings, 1965, 894, text-figs. 5, 6.

Typical *C. manati* had not been reported since the original description by Gruvel based on material brought from the Congo by Dybowski in 1896 until redescribed by the present author from Senegalese material (Stubbings, 1965). Pilsbry (1916) erected two subspecies *lobatibasis* and *crenatibasis* for material that he assigned only tentatively to *C. manati*. Insofar as could be determined these variant specimens probably came from turtles. The greater resistance to penetration of the turtle shell as compared to the skin of the manatee would account for the relatively intact basal margin of the barnacle shell compartments. This has already been shown to happen on the manatee when adjacent individuals overlap (Stubbings, 1965). It is possible, therefore, that *C. manati* occurs on turtles as well as on the type-host but specimens would then be atypical in having a relatively intact basal margin to the compartments. On the other hand a specimen growing by chance on a soft area of the turtle shell or skin would develop branching parietal ribs approximating to the normal type. This is probably what happened in the case of the incompletely known *C. ramosa* described by Korschelt (1933), which may well be a growth form of *C. manati*.

Distribution : embedded in the skin of the manatee *Trichechus senegalensis* in West African estuaries. It may occur also on turtles in W. African waters and if so, owing to the possibility of distribution by currents and wind, it is liable to occur rarely over a much wider range.

Chelonibia patula (Ranzani)

LOCALITIES: Senegal, off Gorée, 99 m. on anchor, coll. Capt. Moloney, B.M. 85.5 (2 shells without soft parts).

Gambia: (1) off Langiang Point on *Callinectes ? marginatus* with *B. venustus*, 10.6.51, coll. M. H. Routh, B.M. 1952.10.2.8 (3 large and 14 smaller spec.); (2) River Gambia, coll. Capt. Moloney, B.M. 01.4 (3 dry shells); (3) off Gunjur, with *B. t. tintinnabulum* from hull of shark-fishing boat, 3.3.52 coll. M. H. Routh, B.M. 1952.10.2.3 (2 spec).

Sierra Leone: (1) 30 m., trawl, from carapace of *Neptunus validus*, 20.9.54, coll. A. R. Longhurst, B.M. 1957.6.3.6 (3 + 7 juv. spec.); (2) 30 m., trawl, from carapace of *Neptunus validus*, 28.9.54, coll. A. R. Longhurst, B.M. 1956.1.7.12 (4 + 3 attached juv. spec.).

Ghana: off Accra: (1) 14 m., with *B. venustus* on shells, 27.4.51 (9 + 8 juv. spec.); (2) 14 m., with *B. venustus* on *Cymbium* shell occupied by a Pagurid, 30.4.51 (3 + 10 juv. spec.); (3) 15 m., on empty *Cymbium* shell, n.d., (1 spec.); (4) on carapace of *Calappa rubroguttata* Herklots, 9.4.51 (2 spec.); (5) 10 m., with *B. venustus* on *Cymbium* fragment, 9.1.52 (2 + 10 juv. spec.); (6) off Chorkor, Accra, 13 m., on *C. rubroguttata*, n.d., (8 + 4 juv. spec.); (7) trawl, on *Cymbium porcinum* with *B. venustus*, coll. E. Salzen, B.M. 1957.6.3.1 (9 + 21 juv. spec.).

Nigeria: (1) Lagos, attached to cork thrown up on beach (dead shells only) (H.G.S.); (2) Bonny River, E. Nigeria, from No. 2 fairway buoy about 3 ft. below water line (13 spec.).

The scutum and tergum have been inadequately figured previously and those of a specimen from Bonny are shown in Text-fig. 23. The scutum (Text-fig. 23*b*, *d*) shows no trace of longitudinal furrows but growth lines are deeply sculptured. On the tergum (Text-fig. 23*a*, *c*) the successive growth increments are demarcated by furrows, the incremental areas being convex in section and ornamented by fine grooves. The mouthparts, likewise inadequately figured, agree with Darwin's description. The

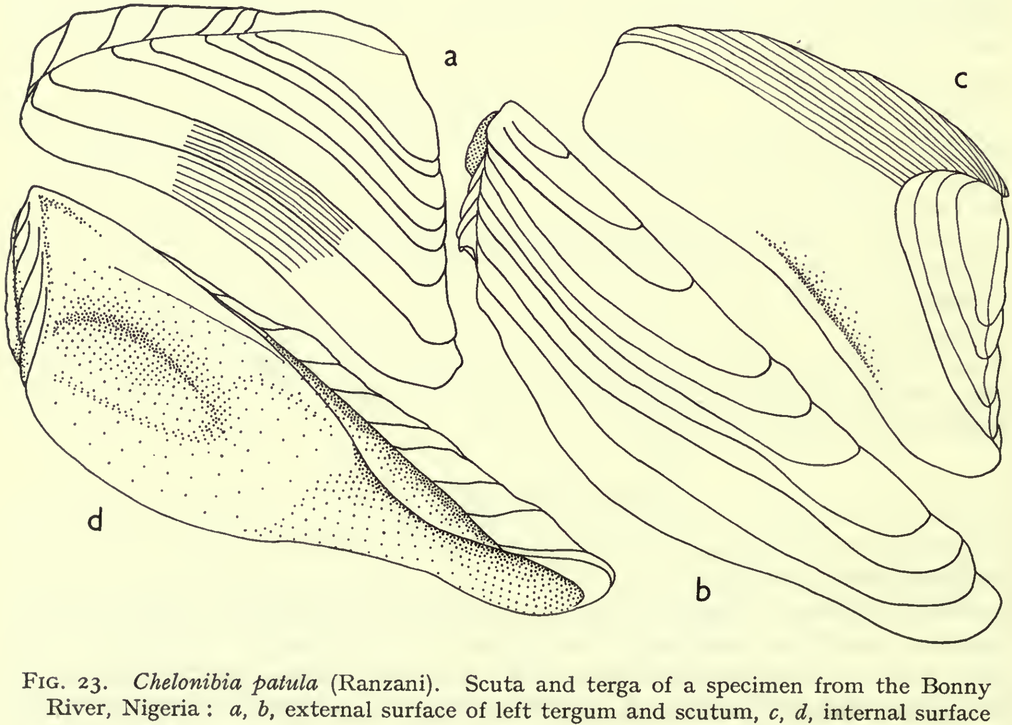


FIG. 23. *Chelonibia patula* (Ranzani). Scuta and terga of a specimen from the Bonny River, Nigeria: *a*, *b*, external surface of left tergum and scutum, *c*, *d*, internal surface of right tergum and scutum. (all ×14).

labrum (Text-fig. 24*a*) is deeply notched, and armed on each side with 20–24 prominent teeth diminishing in size from the midline outwards. The palp (Text-fig. 24*b*) is club-shaped slightly concave on the anterior margin and only sparsely clothed with setae at the distal extremity. The mandibles are 5-toothed. On the specimen dissected (Text-fig. 24*c*) only the 2nd and 3rd teeth bear subsidiary points and not the second and fifth as described by Darwin. The lower angle bears short stout spinules. The first maxilla (Text-fig. 24*d*) is not notched. There are two stout upper spines and a row of lesser spines on the edge. The lower angle is setose. The second maxilla (Text-fig. 24*e*) bears a small oval secondary lobe.

Cirri I and II are short and stout with densely setose and moderately protuberant segments. Cirrus III is intermediate between the first two and cirri IV–VI which

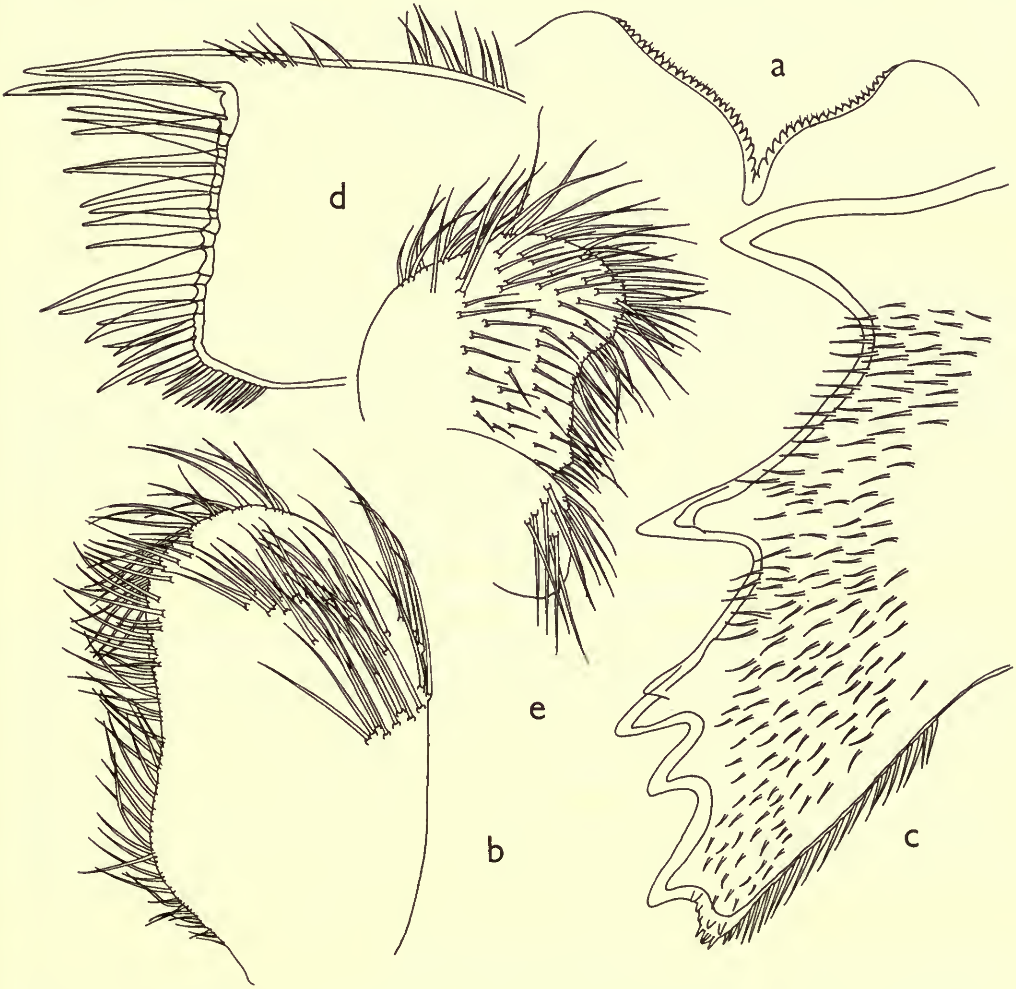


FIG. 24. *Chelonibia patula* (Ranzani) : mouth parts of the same specimen as in Fig. 23 *a*, labrum, *b*, palp (both ×50) ; *c*, mandible ; *d*, maxilla I (both ×80) ; *e*, maxilla II (×50).

are similar. The inward direction of the setae on cirri I–III which lie more on the inner face of the segments and not on their anterior faces is marked. The segmentation of the cirri in the specimen dissected is as follows :

TABLE 10

I	II	III	IV	V	VI
16·15	14·14	20·21	32·33	41·35	41·39

TABLE 10. Segmentation of the cirri of a specimen of *C. patula* from the Bonny River, E. Nigeria.

C. patula is known from French Guinea, Sierra Leone, Ivory Coast, Ghana and Nigeria and presumably therefore occurs throughout subtropical and tropical West Africa. It is commonly found on the larger crabs and Gastropoda, notably old *Cymbium* shells occupied by Pagurids (Gauld, 1957 ; personal observations) and on artifacts such as navigation buoys. It is a sub-littoral shallow-water species, only occasionally cast ashore on floating or sunken debris.

Beyond the west coast of Africa it is known from the Mediterranean and from most tropical and subtropical regions.

Coronula complanata (Mörch)

The authority for including *C. complanata* in the West African fauna would appear to be Pilsbry (1916) who records the presence of some old material labelled West African without name of collector in the U.S. National Museum. But from the tone of the passage the author did not place much reliance on this evidence of provenance. There are no other records for the coast, the nearest being from Table Bay and Simonstown (Barnard, 1924) and the Cape of Good Hope (Nilsson-Cantell, 1932*a*). In the absence of commercial whaling off the coast of West Africa and the very slender chance of a stranded whale with this barnacle being recorded on that coast it is unlikely that confirmatory material will ever be forthcoming.

Platylepas hexastylos (O. Fabr.)

P. hexastylos is not represented in the Ghanaian and Nigerian collections. Records from West Africa are surprisingly few, doubtless due to the unpredictable occurrence and chance collection of the host animals. Specimens are recorded from the Gambia (Darwin, 1854), Mauretania and Morocco (Broch, 1924*b*, 1927 respectively), Sierra Leone and Senegal (Stubbings, 1965). There are more records from the Mediterranean, from turtle hosts.

Elsewhere, *P. hexastylos* is known from the tropical and sub-tropical west Atlantic, from S.E. Asia and from Eastern Australia.

Stomatolepas elegans (O. G. Costa)

Stomatolepas elegans: Pilsbry, 1916, 289, pl. 68, figs. 2, 2*a*.
Stomatolepas elegans: Hiro, 1936, 312, text-figs. 1–5.

The West African status of this species is based on a single specimen in the collections of the Institut Français d'Afrique Noire from *Caretta caretta* (Stubbings,

1965) on which host it was associated with *Chelonibia testudinaria* and *Platylepas hexastylos*.

Hiro (1936) considered that there was only one species, *Stomatolepas elegans* (Costa) and that *S. praegustator* Pilsbry (1910) and *S. transversa* Nilsson-Cantell (1930*b*) were synonymous. The scattered localities recorded by these authors indicate that *Stomatolepas* is widespread in tropical and sub-tropical waters. On the basis of known records it is nowhere common, though this may be a result of the inconspicuous character of the species when embedded in the rough skin of turtles.

Xenobalanus globicipitis Steenstrup

X. globicipitis is of world-wide distribution as might be expected of a species associated with Cetacea. Records for West Africa come solely from the collections of the Institut Français d'Afrique Noire and are all from Senegal (Stubbings, 1965). The nearest other records are those made by the Prince of Monaco in the Atlantic off the mouth of the Mediterranean and in the Azores (Gruvel, 1920).

The cetacean hosts of *X. globicipitis* were listed by Nilsson-Cantell (1930*a*). The IFAN specimens were found on *Delphinus delphis*, *Phocoena phocoena* and *Feresa attenuata*, all except the first being new hosts for this barnacle.

ACROTHORACICA

No species of Acrothoracica were known from West Africa prior to 1957. In that year Gauld reported the occurrence of *Kochlorine hamata* in old shells from the Ghana coast. Subsequently, with increased interest in the Cirriped fauna of West Africa, a further three new species have been described and it would seem highly probable that yet others will be found eventually.

CRYPTOPHIALIDAE

CRYPTOPHIALUS Darwin 1854

Cryptophialus coronatus Tomlinson

Cryptophialus coronatus Tomlinson, 1960, 404, figs. 1–3.

This species was found in the shell of *Haliotis tuberculata* L. from Gorée Island, Senegal. It has not yet been recorded from any other locality.

Cryptophialus variabilis Stubbings

Cryptophialus variabilis Stubbings, 1961*b*, 189, fig. 6.

This species was found in molluscan and *Balanus tintinnabulum* shell rubble from the Island of Principe, Gulf of Guinea.

KOCHLORINIDAE

Kochlorine hamata Noll

LOCALITIES: Ghana: (1–5) Accra: Sta. 10 (5 spec.); Sta. 81 (5 spec.); Sta. 106 (210 spec.); Sta. 107 (266 and 25 spec.); Sta. unknown (249 spec.); (6) Prince's

Town shore (c. 12 spec.); (7) 2 miles west of River Densu, 7·3 m., in shell encrusted with the Polyzoan *Membranipora arborescens* (Canu & Bassler) (3 spec.).

Gulf of Guinea off Annobon: "Calypso" Sta. 107, 1° 26′ 15″ S. 5° 35′ 40″ E., 60 m. in nodule of shell material, 4.7.56 (2, possibly more spec.).

All the Ghanaian specimens except those from Prince's Town and the R. Densu locality were in shells of *Murex bourgeoisi* Tournouer. The number of specimens infesting a shell may be very high, each of the figures (210), (266) and (249) above representing the total number of *Kochlorine* recovered from two infested Gastropod shells, broken up and digested with acid. There may therefore be appreciably more than 100 specimens of *K. hamata* in an infested *Murex bourgeoisi* shell. Living *Murex*, shells occupied by hermit crabs and empty shells are colonized. *Murex* appears to be infested more readily than other gastropod shells. The Prince's Town specimens were recovered from an unidentified fragment of a large thick-walled gastropod shell, bored also by the mollusc *Lithophaga aristata* (Solander).

LITHOGLYPTIDAE

Kochlorine inermis Stubbings

Kochlorine inermis Stubbings, 1964*b*, 343, fig. 5.

This species was described from a single specimen found in the tergum of a small *B. tintinnabulum* taken at Malembe, Angola. As yet there has been no further record of this species.

Kochlorinopsis discoporellae gen. et sp. n.

Localities: Senegal, coll. I. Marche-Marchad (1) South of Gorée I., 38–42 m. in *Cupuladria canariensis* (Busk), 27.10.53: (2) the same, 40–41 m., in *C. canariensis*, 24.2.53; (3) South of Cape Verde Peninsula, 95 m., in *C. canariensis* and *Discoporella umbellata* (Defrance), 18.2.54; (4) Baie de Seminoles, Gorée, 38 m., in *Cupuladria multispinata* (Canu & Bassler) and *D. umbellata*, 8.12.53; (5) SW of Madeleines Light, 48 m., in *D. umbellata*, 15.9.53; (6) " Alignment Gorée-Cap Manuel, lantern de Madeleine, 35–42 m., in *D. umbellata*, 19.10.56; (7) 20–25 miles off Saloum, 35–37 m., in *D. umbellata*, 8.3.55.

Guinea: Parages des Fles de Los, Conakry, 19 m., in *C. multispinata* and *Cupuladria owenii* (Gray), 21.1.53, coll. I. Marche-Marchad; (2) " Calypso " Gulf of Guinea Cruise, Sta. 7, 9° 40′ N., 13° 53′ W., 18 m., in *C. owenii*; (3) Atlantide Sta. 146, 9° 27′ N., 14° 48′ W., 51 m., in *C. canariensis* and *D. umbellata*.

Ivory Coast: " Calypso " Gulf of Guinea Cruise Sta. 17, 5° N., 5° 28′ 30″ W., 27 m., in *C. canariensis* and *D. umbellata*.

Ghana: Accra (1) Sta. 132, 44 m., in *D. umbellata*, 2.5.51; (2) Sta. 133, 51 m. in *D. umbellata*, 2.5.51 (9 spec.).

Gabon: (1) " Calypso " Gulf of Guinea Cruise Sta. 45, 0° 25′ N., 9° E., 73 m., in *Discoporella reussiana* (Manzoni); (2) " Discovery " Sta. 279 off Cape Lopez, 58–67 m., in *C. canariensis*, 10.7.27.

The original specimens from which this new species is described, and the type selected, came from Mr. Bassindale's Sta. 133 off Accra, Ghana, (Bassindale, 1961, text-fig. 2). This is therefore the type locality. Miss P. L. Cook in her study of

West African Cupuladriid Polyzoa (1965*a*) found Acrothoracica in a number of species from several localities. Through her courtesy in passing these to me for study I am able to give the other records listed above. I have to thank Dr. Torben Wolff of the University Zoological Museum, Copenhagen for the use of material from "Atlantide" Sta. 146 off Guinea, which also was recognised by Miss Cook in her examination of the "Atlantide" Cupuladriidae.

Diagnosis: Mantle extremely flattened. No flattened attachment "pad" but the mantle adjacent to the dorsal lip of the orifice is thickened somewhat and protuberant. Mantle with longitudinal and transverse muscles. Orifice slit-like with inner lip armed with bifid or more complex spines. Mouth cirri well developed on long two jointed pedicels with rami of five and four segments. Three pairs of terminal cirri. Caudal appendages present, two-segmented.

TYPES: Holotype BM 1966.12.5.1. paratypes BM 1966.12.5.2–8 from Accra Sta. 133.

The appearance of the orifices of the cavities inhabited by *K. discoporellae* in a zoarium of *D. umbellata* is shown in Pl. 1*a*. The location of the cirripedes within the thickness of the zoarium is revealed by decalcification (Pl. 1*b*).

The mantle is oval, light brown (in spirit) about 3 mm. long by 2 mm. broad and extremely flattened laterally so that the whole animal is somewhat transparent viewed by transmitted light. The orifice is elongated, slit-like and not on a prolongation of the mantle. The margins of the orifice are bordered by setae and short stout "stellate" spines with two or three or more recurved teeth (Text-fig. 25*a*, 26*a*). Towards the ventral side the lips of the orifice are prolonged into short triangular processes. Beyond these the margins carry a row of fine stout spines forming a "comb" collar. The ventral margin of the mantle is crenated. It bears four or five recurved hook-like spines reducing in size posteriorly where several of the typical stellate spines finish the row. In young specimens the antennules can be seen lying close against the dorsal side of the mantle (pl. 1*c*).

The mantle has longitudinal muscle bands running from a little below the orifice toward the opposite end of the mantle parallelling the ventral margin. There are no such muscles over the dorsal half of the mantle which is thin and transparent. The muscles are attached to a thickened band of the mantle delimiting the non-muscular area. The circular muscle system is less developed. Fine muscle bands attached to the thickened attachment process radiate towards the ventral margin of the mantle. In the posterior part of the mantle these muscles run from the thickened band to the ventral margin. Retractor muscles from the orifice run to the body and to the thickened attachment area. These correspond to the retractor corporis and retractor orificii muscles of Utinomi (1950). There is no "retractor *palii rostralis*" (Utinomi 1963). Some of the anatomy as elucidated from a whole mount is shown in Text-fig. 25*b*. There is a single pair of lobe-like processes on the ventral side of the body, probably comparable to the two pairs described by Utinomi (1950) in *Berndtia purpurea*. Mouth cirri, three pairs of terminal cirri and caudal appendages are present. The mouth cirri (Text-fig. 26*e*) have a long two-segmented pedicel, the first segment being greatly elongated. The rami are composed of 5 and 4 segments respectively. A mouth cirrus of another specimen had rami of 7 and 5

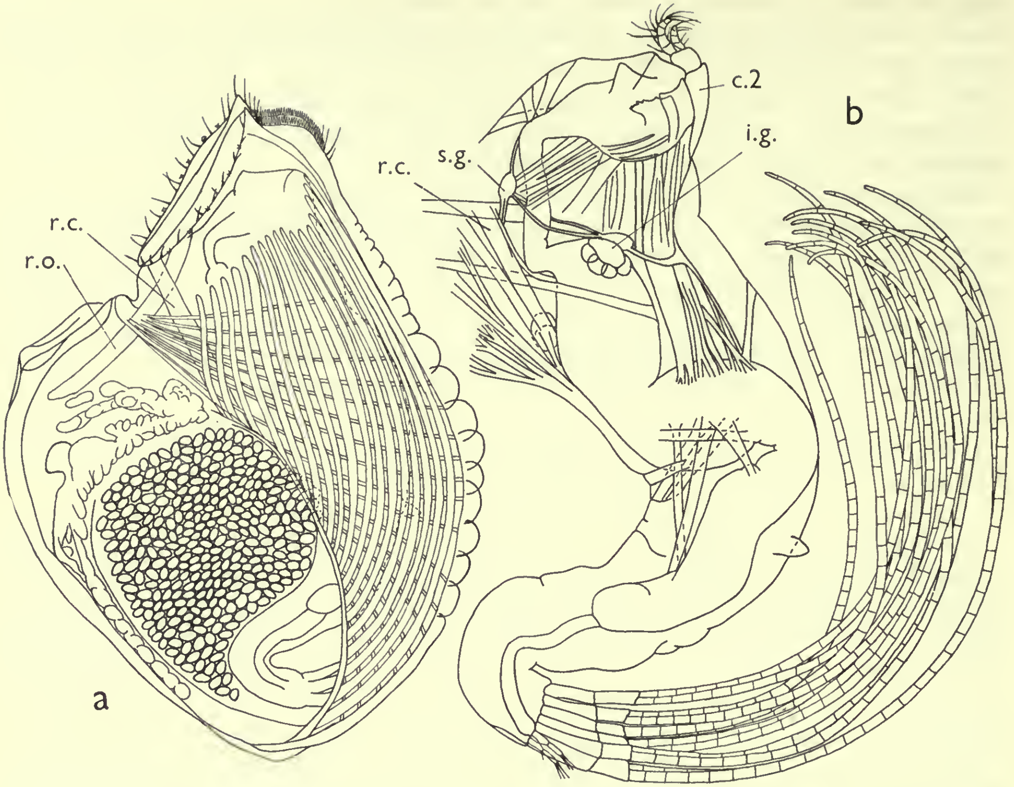


FIG. 25. *Kochlorinopsis discoporellae* gen. et sp. n., *a*, whole animal to show mantle musculature, ovary and egg mass. The broken line within the mantle indicates the ventral surface of the body: the cirri have been omitted (×25); *b*, animal with mantle removed (×38). Setae omitted from the cirri. *C.2* mouth cirrus; *i.g.* infra-oesophageal ganglion; *r.c.* retractor corporis muscle; *r.o.* retractor orificii muscle; *s.g.* supra-oesophageal ganglion.

segments. The terminal cirri are biramous and multi-articulated. The first pair is slightly shorter than the succeeding two pairs. The segments are about twice as long as broad proximally, increasing to about four times as long as broad distally. Each segment bears two pairs of setae anteriorly, the upper pair long and stout, the lower short and fine. Posteriorly each bears a single seta or pair of setae. The caudal appendages are short and two-segmented. The terminal segment bears three short setae.

The labrum is strongly folded so as to embrace laterally the mouth appendages. Its margin is entire and convex and without teeth or hairs. There is a slight suggestion of serration of the margin close to the middle line but there are no teeth. Behind the margin two single lines of long setae run backward parallel to the midline. In a flattened preparation these point towards the middle line but in life they stand more or less upright. There are a few shorter hairs scattered between these lines.

The palps (Text-fig. 26*b*) are very small and conical with a long base of attachment.

They bear a few setae on the outer margin and three or four longer ones at the tip. The mandible (Text-fig. 26*c*) has three simple teeth and a dentate lower angle with about 6 fine teeth. The lower margin has a short row of fine setae.

The maxilla (Text-fig. 26*d*) has a long straight upper margin and short lower margin, the articulation thus being rather long. The anterior margin has a very marked broad notch bearing two stout but short spines. There are two large upper spines strongly curved towards the notch. At their base laterally is a short stout spine similarly curved. The lower and larger part of the anterior edge bears two pairs of short stout spines separated by a gap with short setae. The lower angle is receding and carries a few short spines grading into a few slender setae on the lower margin. There are a few small spines on the surface of the appendages.

The second maxilla is typical of the Acrothoracica, tapering to a point distally and with a very thick outer margin so that the appendage is wedge-shape. The inner margin is concave distally and convex proximally giving the impression of a greatly enlarged lower lobe here. The apical portion is thickly covered with long setae.

Dwarf Male : dwarf males are found in association with most females. One is

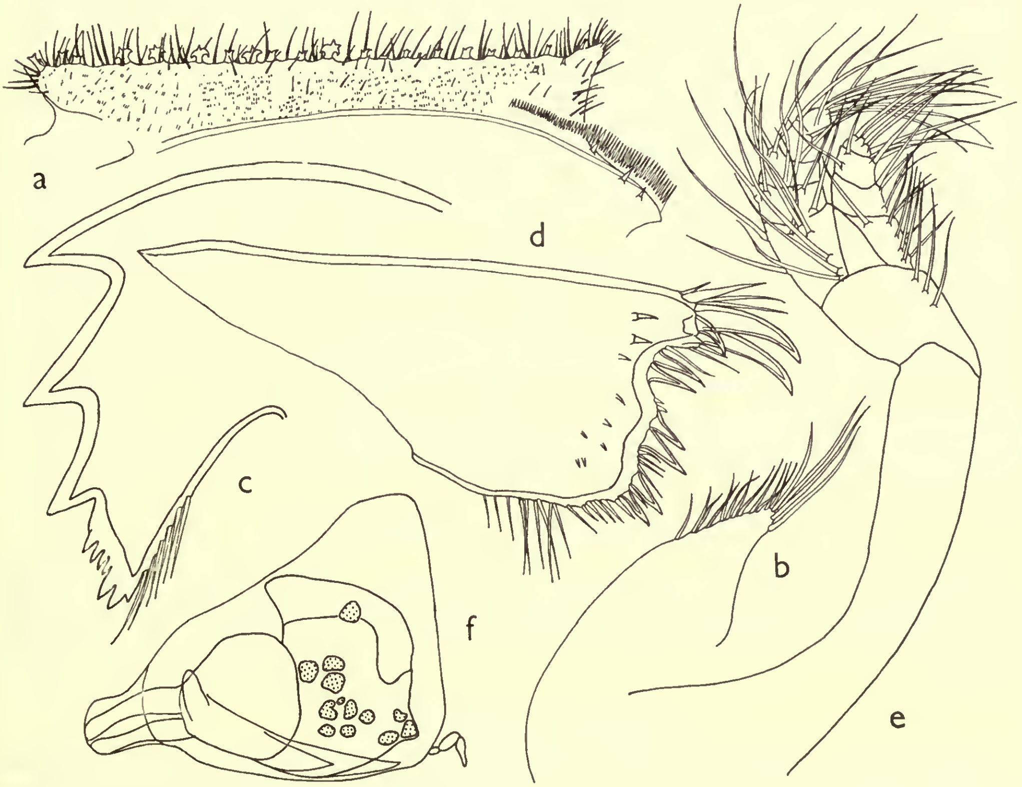


Fig. 26. *Kochlorinopsis discoporellae* gen. et. sp. n., *a,* mantle edge showing spines and comb collar (×93) ; *b,* palp (×170) ; *c,* mandible ; *d,* maxilla I (both ×380) ; *e,* mouth cirrus (×170) ; *f,* dwarf male (×160).

shown in Text-fig. 26*f*. It is triangular in side view, flattened and reminiscent in form of that of *K. hamata* Noll though not so markedly concave on the side opposite the antennae. One two-jointed antenna was present on the specimen. The posterior end is slightly drawn out into a blunt process, presumably the penis sheath. This end of the animal is deeply staining and appears to contain a muscular tube, the penis in the contracted state. The internal anatomy is only partially visible. The penis appears to swell out and fill the posterior part of the organism. There appears to be a wide tubular structure lying near the surface close to the margin between penis and antenna, probably the vesicula seminalis. A number of deeply staining irregular or rounded bodies in the opposite half of the animal are presumably lobes of the testis.

The dimensions of this specimen were length 0·33 mm. depth 0·20 mm.

In having well-developed mouth cirri, an attachment disc, short labrum and no lateral bar this species resembles both *Lithoglyptes* and *Kochlorine*. *Lithoglyptes* has four pairs of terminal cirri as against three pairs in *Kochlorine*. On this basis the present species should be referred to *Kochlorine*. The absence of the long retractor muscle along the rostral side of the mantle (" retractor pallii rostralis " of Utinomi, 1963) is against this. The genera *Kochlorine* and *Balanodytes* both have this prominent paired muscle band which Utinomi (1963) and Tomlinson (1963) consider as diagnostic of the family Kochlorinidae. Utinomi considers (1963 : 70) that the number of pairs of cirri and the presence or absence of caudal appendages should be regarded as of generic value only and that the musculature is a better criterion of family relationships. On this basis *K. discoporellae* should be assigned to the Lithoglyptidae (Aurivillius, 1894 ; emend. Tomlinson & Newman, 1960) as " retractor corporis " and " retractor orificii " muscles are present. This procedure demands, however, a further amendment of the family diagnosis to include forms with only three pairs of terminal cirri. Furthermore inclusion of this species in *Lithoglyptes* would entail redefining this genus. Hence it is proposed to erect a new genus within the Lithoglyptidae to contain species with only three pairs of terminal cirri. The species is accordingly named *Kochlorinopsis discoporellae* g. et sp. n., recording its cirral affinity with *Kochlorine* and its association with the Polyzoan *Discoporella umbellata*. The diagnoses of family and genus follow :

Family **LITHOGLYPTIDAE** emend.

Mouth cirri well-developed, the pedical two-jointed. Three to five pairs of terminal cirri, if less than five pairs, then caudal appendages present. No gut teeth or gizzard. No lateral bar. Attachment disc present, retractor orificii and r. corporis muscles present.

Genus ***KOCHLORINOPSIS*** nov.

Lithoglyptidae with three pairs of terminal cirri : caudal appendages present, two-jointed : mouth cirri with number of segments in rami varying from five and four to seven and five.

TYPE, *K. discoporellae* nov.

3. THE WEST AFRICAN CIRRIPED FAUNA

From geographical plots of the distribution of the various species it is possible to distinguish several groups of species in which the individual members have approximately the same limited geographical range. Other species are apparently cosmopolitan. A considerable number are still insufficiently known for their geographical range to be determined.

The following groups of species can be distinguished :

(1) *Northern species* (Text-fig. 27A)

Species with a wide range in latitude extending from high latitudes in the northern hemisphere into sub-tropical and tropical waters. Two species only have this distribution, *Scalpellum scalpellum* (L.) and *Chthamalus stellatus stellatus* (Poli). *S. scalpellum* ranges south to the Congo and Angola. The main distribution of *C. stellatus* appears to end in the latitude of Dakar (Cape Verde) though small numbers have been recorded from as far south as Angola. It is probable, however, that the records of this species from south of the Bight of Biafra, as well as those from the Eastern Mediterranean are erroneous and due to misidentifications.

(2) *Western English Channel to the Gulf of Guinea* (Text-fig. 27B–D)

In this series are included species with a northern limit of distribution in the south-west English Channel, on the Atlantic coast of Europe or in the Western Mediterranean and which extend southwards through the Gulf of Guinea. In this category, in order of diminishing northward distribution fall :

Pyrgoma anglicum Sowerby
Balanus perforatus Bruguière
B. spongicola Brown
B. tulipiformis Darwin
B. fallax Broch

Much of the geographical range of *P. anglicum* coincides with that of *B. perforatus*, the major differences being the extension of the range of *B. perforatus* into the Eastern Mediterranean and south of the Gulf of Guinea and the presence of *P. anglicum* in the Cape Verde Archipelago where *B. perforatus* is hitherto unknown.

(3) *South-west Europe to Cape Verde* (Text-figs. 27D, 28A)

Species distributed from the Atlantic coast of Europe or the Western Mediterranean to the region of Cape Verde only.

Mitella pollicipes (Gmelin)
Heteralepas cornuta (Darwin)
Paralepas minuta (Philippi)

H. cornuta is still further restricted in distribution in that it is known only from north-west Africa, from Morocco to the Cape Verde Islands.

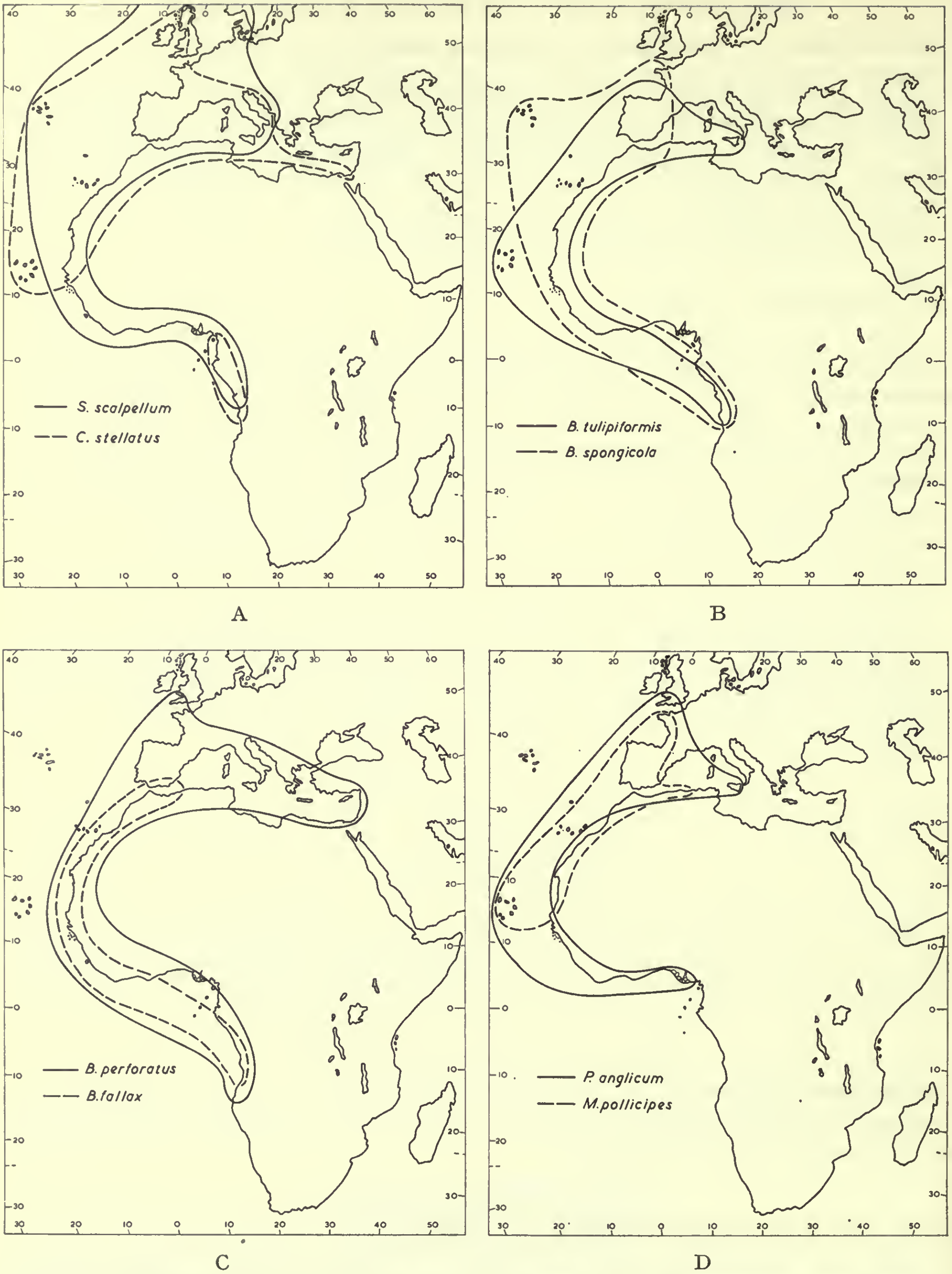

S. scalpellum
C. stellatus
A
B. tulipiformis
B. spongicola
B
B. perforatus
B. fallax
C
P. anglicum
M. pollicipes
D

FIG. 27. Distribution of some West African barnacles. A. The northern components *Sc. scalpellum* (L.) and *C. stellatus* (Poli). The far northern distribution of *Sc. scalpellum* is omitted. The eastern Mediterranean distribution and that south of the Gulf of Guinea for *C. stellatus* may be erroneous due to mis-identifications. B, C, D, South-west Europe, Western Mediterranean, North-west and West African species. *B. perforatus* extends also to the Eastern Mediterranean.

(4) *Endemic West African species* (Text-fig. 28B, C)

There are only five species that can be regarded as possibly endemic in tropical West Africa :

Smilium renei (Gmelin)
Ibla atlantica sp. n,
Chelonibia manati Gruvel
Balanus pallidus Darwin
Chthamalus aestuarii Stubbings

S. renei, C. manati and *B. pallidus* extend northwards to Dakar ; *C. aestuarii* is not known as yet north of Sierra Leone and *Ibla atlantica* only from off Sierra Leone. The known southern limit of all except the *Ibla* is northern Angola. *B. pallidus* is an abundant intertidal species in West Africa. There are a few records from other parts of the old world (" P " in Text-fig. 28*c*), but these could be instances of ship-borne introductions or even misidentifications. Darwin (1854) mentioned seeing specimens of *B. pallidus* " from the West Indies ". Specimens from Cananéia, S. Paulo, Brasil received through the kindness of Dr. V. Zullo are of this species, which may, therefore, occur naturally on both sides of the tropical Atlantic.

It is possible that *B. tintinnabulum zebra* is a West African variety but here again it may well be that the pattern of its natural distribution, which is very imperfectly known, is blurred by records of ship-borne specimens.

(5) *South African species* (Text-fig. 28D)

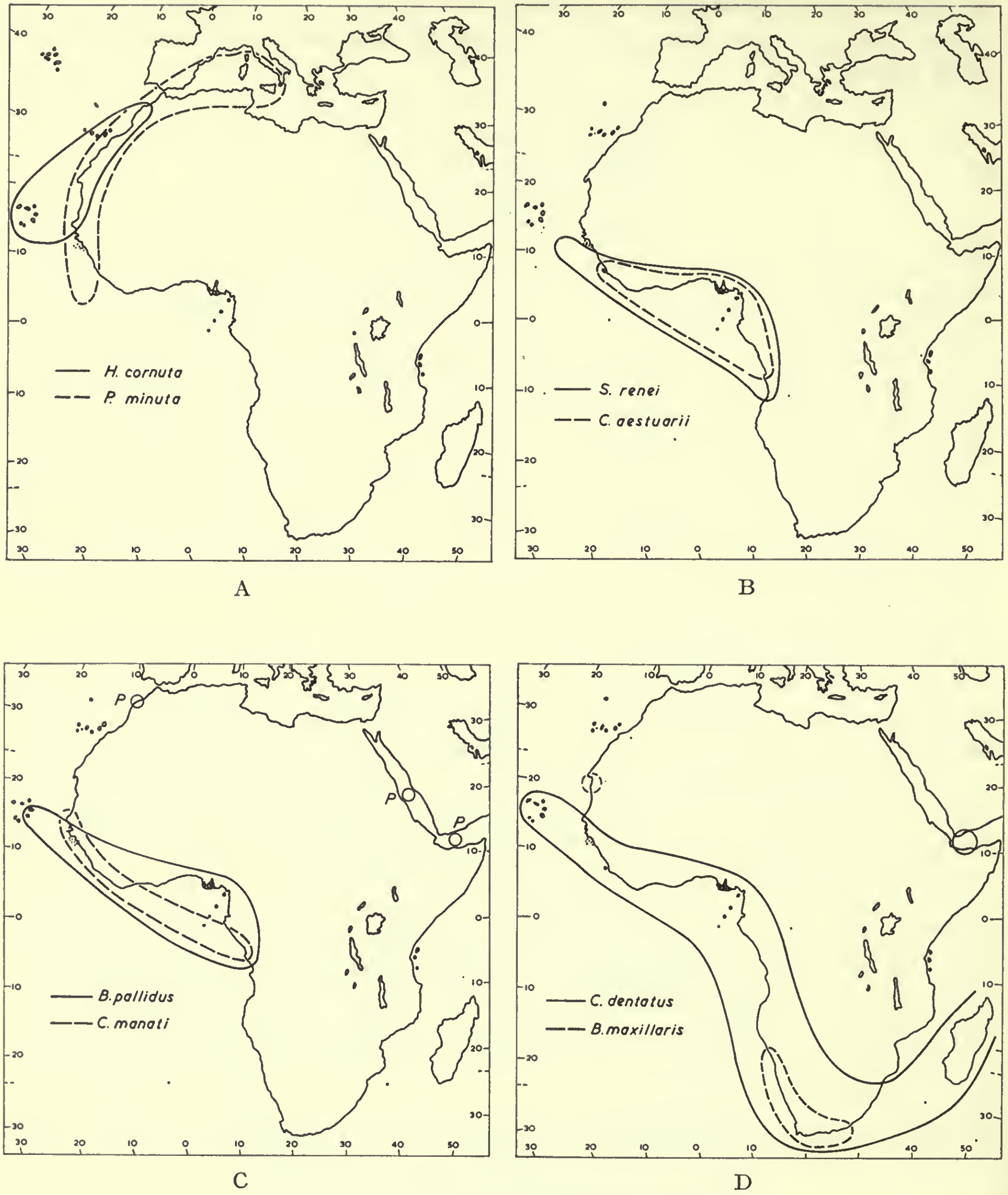
Only two species can be considered as South African with an extended distribution northward in the Atlantic namely *Chthamalus dentatus* and *Balanus maxillaris* but the evidence is not clear cut. *C. dentatus* is a common species at the Cape and on exposed coasts in West Africa as far as Dakar. It is recorded from several widely spread Indian Ocean localities so should perhaps be regarded as an Indian Ocean form that has penetrated to the Atlantic. Until records for the Indian Ocean are much more numerous, however, its true status is debatable.

It is questionable whether *B. maxillaris* is native to West Africa. It is well-known at the Cape but the sole record north of Angola is for Port Etienne, Mauretania, which suggests that this may be a chance introduction. Further records from Gough Island and between South America and the Falkland Islands in the South Atlantic (Nilsson-Cantell, 1939*a*) suggest that *B. maxillaris* may be really a southern temperate species widespread in those latitudes as suggested by Kolosvary (1943*b*).

(6) *Circumtropical species*

Several species are known from the tropics of both the old and new world :

Trilasmis (*Poecilasma*) *kaempferi* (Darwin)
Octolasmis lowei (Darwin)
B. amphitrite amphitrite Darwin
B. calceolus Darwin (old world tropics only)
B. tintinnabulum tintinnabulum (L.)
B. trigonus Darwin
B. venustus Darwin


H. cornuta
P. minuta
S. renei
C. aestuarii
P
P
P
B. pallidus
C. manati
C. dentatus
B. maxillaris

A B

C D

FIG. 28. Distributions of African species: A, temperate-subtropical Western Mediterranean and N.W. African: B, C, West African–Gulf of Guinea tropical species. Three isolated reported occurrences of *B. pallidus* in North-west Africa, the Red Sea and Gulf of Aden are ringed and marked with a "P": D, the temperate South-African element —*C. dentatus* Krauss extending throughout tropical West Africa and the southern *B. maxillaris* with a single record from the Cap Blanc region.

The inclusion of *O. lowei* in this group is dependent upon the interpretation of the synonymy of this species. If the Western Atlantic and Pacific specimens are conspecific with those of the Eastern Atlantic then the species is certainly circumtropical.

B. venustus Darwin is present on the whole West and South African coast from Port Etienne, Mauritania to Natal, with an outlying northern record from Cadiz Bay, southern Spain. It is particularly abundant off Ghana and this might well be the centre of distribution of the species. The picture is complicated, however, by an isolated series of records in the Bay of Bengal from Ceylon, to Akyab in Burma. There are no East African or Arabian Sea records linking these two areas.

(7) *Deepwater elements*

The few species so far collected from beyond the continental shelf indicate the presence of a deep-water barnacle fauna here as elsewhere. The following five species are the only ones so far recorded :

Smilium longirostrum (Gruvel)
Scalpellum imperfectum Pilsbry
S. trapezoideum Hoek
S. velutinum Hoek
Verruca striata Gruvel

By comparison with the known fauna of the Azores region it may be expected that many others await discovery.

(8) *Introduced species*

Several species recorded sporadically are well-known to have spread from their original homes by the unwitting agency of man. Others may have spread in the same way but have not been detected. The following species, found sporadically in West Africa, may have this doubtful status.

Octolasmis hoeki (Stebbing)
Chthamalus fragilis Darwin
C. stellatus bisinuatus Pilsbry
Balanus eburneus Gould
B. venustus niveus Darwin
B. nigrescens Lamarck
B. tintinnabulum concinnus Darwin

The first five have representatives in North and Central American waters, the two Balani most probably having been spread from there by man. *B. nigrescens* was probably introduced from the western Pacific. *B. tintinnabulum* may also have been introduced on ships from that ocean. Two further varieties, *B. t. azoricus* Pilsbry and *B. t. spinosus* (Gmelin) may also be incomers, the first from the Azores presumably being carried by ships. *B. t. spinosus*, as suggested elsewhere (Stubbings, 1961*b*) is perhaps another island race that occasionally reaches the African mainland.

There is left a number of species recorded from West Africa for the distribution of which there is wholly inadequate knowledge. The very few records from African waters (in many instances only a single record) are inadequate to establish these as

W. African species. The following all require confirmation from new finds :

Trilasmis (*Poecilasma*) *crassum* (J. E. Gray)
Octolasmis tridens (Aurivillius)
Chthamalus stellatus bisinuatus Pilsbry
Pachylasma gigantea (Philippi)
Balanus tintinnabulum maroccana Broch
B. amphitrite albicostatus Pilsbry
Tetraclita divisa Nilsson-Cantell
T. purpurascens Wood
T. squamosa squamosa (Brug.)

In considering the above groupings of species the pelagic species of *Lepas* and *Conchoderma* and those species found on turtles or cetaceans have been excluded. The wide-ranging habits of the host animals or the drift of floating debris used as a support render specific zoogeography of these barnacles valueless. The one exception has been *Chelonibia manati* ; the estuarine habitat and sluggish habits of the sirenian preclude long migrations.

After removal of these nine species, the deep water species, the introduced species and those with imperfectly known distribution, some 24 species are left for which the zoogeographical information is more or less adequate. Three of these species, *T. kaempferi*, *B. t. tintinnabulum* and *B. trigonus* are circumtropical. Two, *B. v. venustus* and *B. calceolus* and possibly a third *B. a. amphitrite* are old world tropical species but have a restricted Atlantic distribution. They have been placed in Table II with species of similar distribution. Where a species is apparently at the limit

TABLE II

Species	S.W. Europe	W. Med.	N.W. Afr.	W. Afr.	S.W. Afr.	S. Afr.
Sc. scalpellum . .	+	+	+	+	+	—
B. perforatus . .	+	+	+	+	(+)	—
Ch. stellatus . .	+	+	+	(+)	—	—
B. tulipiformis . .	+	+	+	+	—	—
B. spongicola . .	+	+	+	+	—	—
P. anglicum. . .	+	+	+	+	—	—
M. pollicipes . .	+	+	+	—	—	—
P. minuta . . .	—	+	+	(+)	—	—
B. a. amphitrite . .	—	+	+	+	—	—
B. calceolus . . .	—	+	+	+	—	—
B. fallax . . .	—	+	+	+	(+)	—
B. v. venustus . .	—	(+)	(+)	+	—	+
H. cornuta . . .	—	—	+	(+)	—	—
O. lowei . . .	—	—	+	+	—	—
B. pallidus . .	—	—	(+)	+	—	—
Ibla atlantica . .	—	—	—	+	—	—
S. renei . . .	—	—	—	+	—	—
Ch. aestuarii . .	—	—	—	+	—	—
C. manati . . .	—	—	—	+	—	—
Ch. dentatus . .	—	—	—	+	+	+
B. maxillaris . .	—	—	(+)	—	+	+
Totals . . .	7	12	16	19	5	3
% . . .	37	63	84	100	26	16

TABLE II. The northward and southward Atlantic distribution of 21 tropical West African barnacles.

of its range in an area the " plus " symbol for presence is placed in brackets thus (+).

The northern affinities of the West African cirriped fauna are obvious. Of the remaining 19 species occurring between Dakar and Lobito, Angola, and listed in the table below, 16 (84%) occur to the north of Dakar and 12 of these (63%) extend into the western Mediterranean. Only one species, *B. perforatus*, is known reliably from the Eastern Mediterranean. Although a second, *C. stellatus*, is recorded from there this may well be an error of identification. Seven species (37%) extend into S.W. Europe, with a few reaching the English Channel. On the other hand only 5 (26%) are known from S.W. Africa and 3 (16%) from the Cape.

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SUMMARY

1. The distribution of seventy species and varieties of barnacles, including five species of Acrothoracica in West Africa is recorded.

2. Two new species are described. *Ibla atlantica* sp. n. from the continental shelf off Sierra Leone represents the first record of this genus in the Atlantic. A new Acrothoracican, *Kochlorinopsis discoporellae* gen. et sp. n. has characters between *Kochlorine* and the Lithoglyptidae. It is referred to the latter family, for which a redefinition is given.

3. The type material of *Dichelaspis hoeki* Stebbing and *D. antiguae* Stebbing has been re-examined and compared with new material. The union of the two species as *D. hoeki* by Annandale (1910), followed by Nilsson-Cantell (1927) (as *O. hoeki* (Stebbing)) is rejected and *D. antiguae* is reinstated as a species, *O. antiguae* (Stebbing). It is not, as far as is known, found in the eastern Atlantic.

4. The forms *Balanus amphitrite communis*, *B. a. hawaiiensis* and *B. a. denticulata* as found in W. Africa, have been re-examined in the light of Harding's (1962) redescription of Darwin's type material. No constant differences could be detected on which to separate the varieties and they are united as *B. amphitrite amphitrite* Darwin.

5. Harding (1962) could not find constant differences for separating the two " *amphitrite* " varieties called by him *B. pallidus pallidus* Darwin and *B. pallidus stutsburi* Darwin. The latter name is reduced to a synonym and both white and coloured shells are referred to the species *B. pallidus* Darwin.

6. Amplified descriptions have been given of the following : *Chthamalus dentatus* Krauss, *C. aestuarii* Stubbings, *Balanus perforatus* Bruguière, *B. venustus venustus* Darwin, *B. fallax* Broch, *Tetraclita divisa* Nilsson-Cantell and *Chelonibia patula* (Ranzani).

7. The affinities of the West African barnacle fauna with those of South-west Europe, the Mediterranean and South Africa are discussed.

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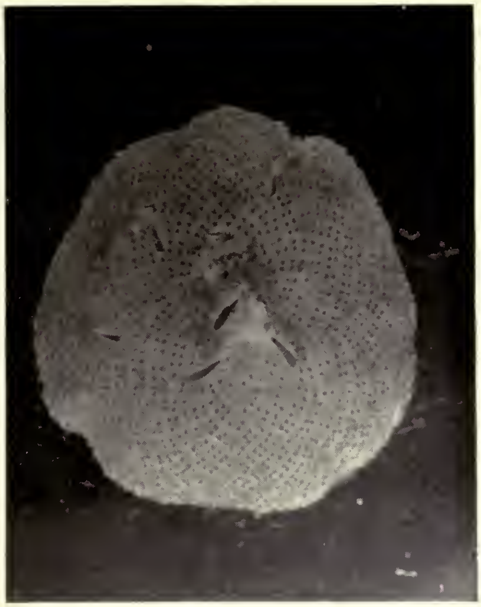
PLATE 1

Kochlorinopsis discoporellae g. et sp. n.

a. Frontal view of a specimen of a host Polyzoan *Discoporella umbellata* (Defrance) with a number of embedded *K. discoporellae* ×4.

b. Basal view of the same after decalcifying with diluted hydrochloric acid so that the embedded cirripedes of various sizes can be seen ×4.

c. A recently settled specimen of *K. discoporellae* photographed by transmitted light showing the paired antennules lying against the dorsal side of the mantle ×54.



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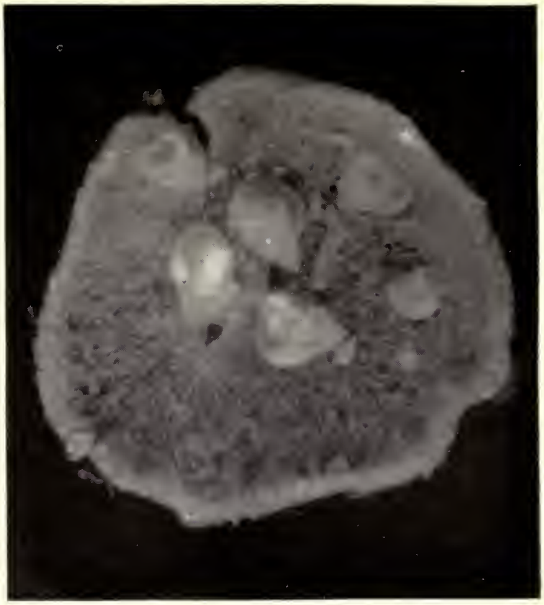

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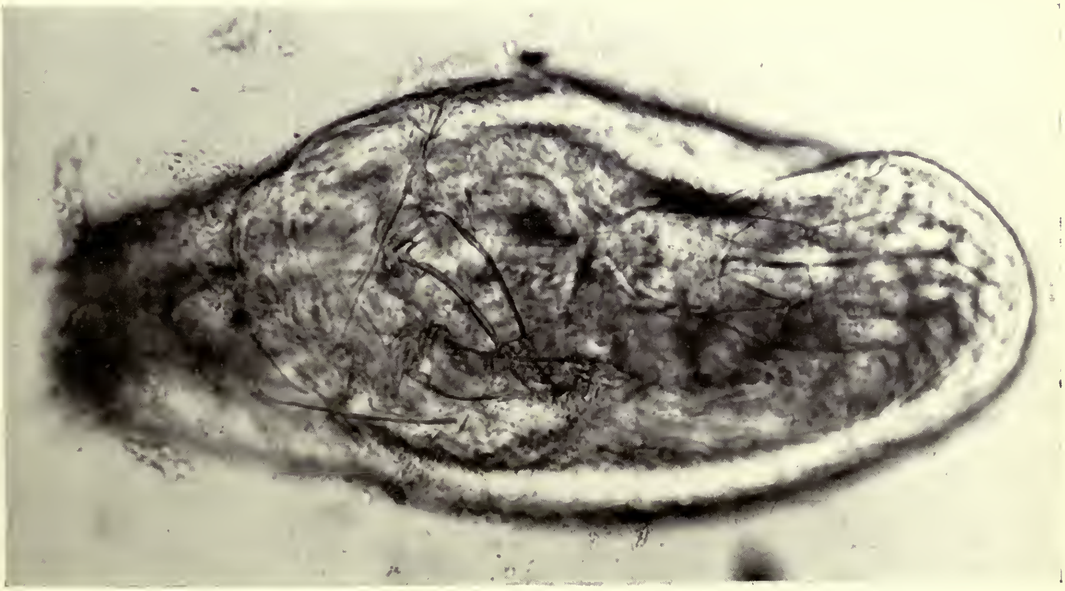

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POLYZOA (BRYOZOA) FROM WEST AFRICA
THE PSEUDOSTEGA, THE CRIBRIMORPHA AND SOME ASCOPHORA IMPERFECTA

PATRICIA L. COOK

BULLETIN OF
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ZOOLOGY Vol. 15 No. 7
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BRITISH MUSEUM
29 NOV 1967
NATURAL HISTORY

BY

PATRICIA L. COOK

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By PATRICIA L. COOK

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INTRODUCTION

THE Collections from which specimens are described here comprise the " Calypso " Collection I, from Senegal and the Bay of Biafra, and Collection II, from the Cape Verde Islands; the Marche–Marchad Collections, from Senegal and the Achimota Collections, from Ghana, see Cook (1964*a* : 44). Some additional specimens from the west African Expeditions of the " Atlantide ", and " Galathea ", and from west African Stations from the Mortensen Java–S. Africa Expedition, all of which are stored at the Universitetets Zoologisk Museum, Copenhagen, are also included. The holotypes of new species, together with representative specimens of all the material described are deposited in the British Museum (Natural History), unless otherwise stated.

Specimens were treated with eau de javel for examination of calcareous parts, and decalcified to show chitinous parts. The following measurements were made where possible:

Lz	Length of zooid	lz	Width of zooid
Lor	Length of orifice	lor	Width of orifice
Lfo	Length of fertile orifice	lfo	Width of fertile orifice
Lop	Length of operculum	lop	Width of operculum
Lov	Length of ovicell	lov	Width of ovicell
Le	Length of embryo	le	Width of embryo
Lan	Length of ancestrula	lovor	Width of ovicellular orifice
Lav	Length of avicularium		
Lm	Length of mandible		

Specimens in the Collection of the British Museum (Natural History) are referred to by their registered numbers, thus: 1964. 3. 20. 15.

The Pseudostega are represented by 5 species, 3 of which occur south of the Canary Islands; the number of species of Cribrimorpha is also small, only 3 being represented. The Ascophora Imperfecta includes those genera in which the operculum and contiguous frontal membrane are covered by an overarching frontal shield (see Harmer, 1957 : 645). A true compensation-sac is therefore absent. There is evidence that at least 2 distinct types of development of the frontal shield exist, and examples of both have been found in the genera in these Collections. The first type resembles that seen in *Tremogasterina* (see Powell & Cook 1967), which appears to indicate affinities with some Cribrimorpha (see pp. 337, 342). The second type is that originally described in *Umbonula* by Harmer (1957) for the Ascophora Imperfecta (see pp. 345, 347).

Division **PSEUDOSTEGA** Levinsen

CELLARIA Ellis & Solander

Cellaria Ellis & Solander, Harmer, 1923 : 301; Hastings, 1947; Lagaaij, 1952 : 47, Galopim de Carvalho, 1963.

Zoarium free, erect, cylindrical, typically jointed, with chitinous rootlets. Opesiae reduced, scarcely larger than the orifice. Avicularia vicarious. Ovicells entotoichal.

The characters used to define species in this genus need further study, and a complete revision of the Atlantic and Mediterranean " species ", at least, is urgently required[1].

Two species of *Cellaria* were recorded by Calvet (1907 : 400–401) from the north-west African region. These were *C. salicornioides* (Lamouroux), from north-west Morocco (from 636 m.), and *C. fistulosa* (Linnaeus) from the Canary Islands (from 3700 m.). Norman (1909) recorded *C. fistulosa* from Madeira, from " deep water ", and also listed *C. johnsoni* (Busk). His specimen labelled with this name is referable to *C. salicornioides* " var. *normani* " (see below). *C. salicornioides* and *C. fistulosa* were recorded by Canu & Bassler (1928*b* : 25) from Morocco. *C. fistulosa* has not been found to occur in these west African Collections, its most southerly limit appears to be the Canary Islands. *C. sinuosa* (see below) does not appear to occur south of Tangier.

---

[1] A discussion of *Cellaria*, with descriptions of several species has recently been given by Prenant & Bobin (1966 : 372).

Cellaria fistulosa auctt. (non Linnaeus)

(Text-fig. 1)

Cellularia fistulosa (Linnaeus) Norman, 1909 : 292, Madeira. Canu & Bassler, 1928*b* : 25, Morocco, 28–155 m., sandy bottom.
Cellaria fistulosa auctt. (non Linnaeus) Harmer, 1923 : 302.

MATERIAL EXAMINED. B. M. Coll. Madeira, 1911. 10. 1. 772, 3 worn fragments, Norman Coll. Pedra da Malha, off Porto Santo, 55 fath. 1910. 10. 30. 21, Kirkpatrick Coll. Off Tangier, 1903. 4. 29. 10A and 16, 30–40 fath.

DIMENSIONS. (African material). Lz 0·50–0·55 mm., lz 0·24–0·26 mm., Lor 0·12–0·14 mm., lor 0·07–0·09 mm. (Ovicelled zooids, av. Lz 0·50 mm., lz 0·29 mm., Lovor 0·10 mm., lovor 0·06 mm.) Lav 0·12–0·14 mm., lav 0·14–0·15 mm., Lm 0·04–0·05 mm., lm 0·08–0·09 mm. Av. L internode, 9 mm.

Zoarium with short internodes, chitinous joints tubular. Orifice near the middle of the zooid, with small, paired, proximal denticles. Ovicellular orifices oval. Avicularia with small rounded mandibles directed distally, or slightly distal-laterally.

Cellaria fistulosa auctt. is not the same species as that introduced by Linnaeus. I here follow Lagaaij (1952) in using the name *C. fistulosa* auctt. in the sense restricted by Harmer (1923), pending a full revision of the genus.

Cellaria sinuosa (Hassall)

(Text-fig. 2)

Cellaria fistulosa (Linnaeus, non auctt.), Harmer, 1923 : 303.
Cellaria sinuosa (Hassall), Lagaaij, 1952 : 48, pl. 4, figs. 4, 5, Pliocene, Europe.

MATERIAL EXAMINED. B. M. Coll. Off Tangier, 1903. 4. 29. 10B, 30–40 fath.

DIMENSIONS. Lz 0·45–0·56 mm., lz 0·23–0·26 mm., Lor 0·06–0·08 mm., lor 0·10–0·12 mm. (Ovicelled zooids, av. Lz 0·50 mm., lz 0·24–0·26 mm. Lovor 0·02–0·04, lovor 0·07–0·09), Lav 0·12–0·17 mm., lav 0·16–0·20 mm., Lm 0·07–0·09 mm., lm 0·13–0·15 mm., Av. L internode, 15 mm.

Zoarium robust, with very long internodes, chitinous joints tubular. Orifice in the distal half of the zooid, with a prominent proximal lip. Minute distal and proximal denticles present. Ovicellular orifice transverse, frequently slit-like. Avicularia small, mandibles rounded, directed distally.

C. sinuosa has long internodes, and a robust zoarium, like that of *C. elongatoides* (see below). It does not seem to occur south of Tangier, and, like *C. fistulosa*, has not been reported from the more southerly parts of the west African coast.

Cellaria salicornioides " var. ***normani*** " Hastings

(Text-fig. 3)

Cellularia nodosa (d'Orbigny) Norman, 1909 : 293, pl. 42, figs. 4, 5, Madeira (not *C. nodosa* d'Orbigny, 1851 : 31).
Cellularia johnsoni (Busk), Norman, 1909 : 293, Madeira.
Cellaria salicornioides var. *normani* Hastings, 1947 : 221, pl. 2, fig. B.

MATERIAL EXAMINED. Marche–Marchad Coll. II. 30D, Sud de Baie de Gorée, 18.ii.54, 95 m. Coll. III. 28J, dragage 4, " Gerard Freca " 18.ii.54, 97–98 m.

Achimota Coll. II, Stn. 117, Trawl 2, 5.iv.51, 64 m, 13E.

Copenhagen Museum. " Atlantide " Coll, Stn 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m., 45R.

British Museum. Holotype of *C. nodosa* Norman, 1911.10.1.777, Madeira. Paratype of *C. nodosa*, 1911. 10. 1. 778, Madeira, Norman Coll. As *C. nodosa*, Porto Santo Is., 65 fath., 1945. 7. 10. 4 and 1910. 10. 30. 18, Kirkpatrick Coll. As *C. johnsoni*, Madeira 30–70 fath., 1911. 10. 1. 733, Norman Coll. Gulf of Guinea, 1964. Redier Coll.

DIMENSIONS. Lz 0·23–0·40 mm., lz 0·14–0·21 mm., Lor 0·05–0·06 mm., lor 0·06–0·09 mm., (Ovicelled zooids av. Lz 0·41 mm., lz 0·25 mm., lovor 0·07 mm.), Lav 0·46–0·50 mm., lav 0·21–0·23 mm., Lm 0·14–0·16 mm., lm 0·17–0·19 mm. Av. L internode, 6 mm.

Zoarium slender, fertile parts wide and conspicuous, chitinous joints tubular. Branches frequently formed by lateral offsets, rather than by dichotomy. Zooids elongated. Orifice curved proximally, without denticles. Ovicellular orifice cresentic. Avicularia large, rostrum rounded distally, raised. Mandible directed distally.

C. salicornioides " var. *normani* " has been fully discussed by Hastings (1947). Approximately half the branches in these specimens are formed by lateral offsets, the remainder being the result of dichotomous branching. The internodes are all more slender than those of typical *C. salicornioides*, and the west African material has therefore been referred to the variety, as has Norman's material labelled " *C. johnsoni* ", see above. It seems doubtful, however, that the form can rank as a subspecies.

A large number of colonies, collected by Kirkpatrick from Madeira (Agua de Baixa, off Porto Santo Is., 65 fath., 1910. 10. 30. 18), illustrate the method of growth. They originate on small Gorgonid stems, and grow in profusion, accompanied by Ascidians, worm tubes, Foraminifera, Sertularian Hydroids and small Lamellibranch Molluscs. The *Cellaria* internodes are themselves encrusted at the base by a Sponge.

Cellaria elongatoides Bassler

(Text-fig. 4)

Cellaria elongata Canu & Bassler, 1928*b* : 24, pl. 2, figs. 7–9, Morocco, 170 m. (preoccupied by *C. elongata* Canu, 1908, a south American fossil species).
Cellaria elongatoides Bassler, 1936 : 161 (for *C. elongata* Canu & Bassler, 1928).

MATERIAL EXAMINED. " Calypso " Coll. I, Stn. 1, 21° 05′ N., 17° 14′ W., 10.v.56, 43–45 m., C52A.

Marche–Marchad Coll. II. 4A, 8A, 12E, 27A, Large de Gorée, 5.vii.55, 50 m., 7L, Baie de Gorée, 50–100 m., 32J, Sud de presque l'Ile de Cap Vert, 18.ii.54, 95 m. Coll. III. 28D, dragage 4, " Gerard Freca ", 18.ii.54, 97–98 m.

Achimota Coll. II. Stn. 117, Trawl 2, 5.iv.51, 64 m., 13D.

Copenhagen Museum, Grand Canary, 24.iii.30, 15–20 fath., 89M, Mortensen Coll.

" Atlantide " Coll., Stn. 60, 5° 06′ N., 9° 34′ W., 9.i.46. 54A. Stn. 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m. 45R. Stn. 161, off Bathurst, Gambia, 24.iv.46, 18 m. 58C. Stn. 163, 13° 43′ N., 17° 23′ W., 25.iv.46, 65–89 m. 60C.

DIMENSIONS. Lz 0·40–0·45 mm., lz 0·29–0·32 mm., Lor 0·07–0·09 mm., lor 0·15–0·18 mm., (Ovicelled zooids av. Lz 0·55 mm., lz 0·32 mm., lovor 0·10–0·11 mm.), Lav 0·09–0·10 mm., lav 0·11–0·12 mm., Lm 0·03–0·04 mm., lm 0·11–0·12 mm. Av. L internode 11 mm.

Zoarial internodes frequently very long (longest observed 20 mm.), and curved, chitinous joints tubular. Zooids wide, their boundaries well-marked. Orifices with large, paired proximal denticles. Ovicellular orifices with a large proximal denticle. Avicularia small, not common, rostrum sub-triangular, very slightly raised distally. Mandible semi-circular, directed distally.

The most striking characters of this species are the large oral denticles and the small avicularia. *C. elongatoides* is a robust species, and the zoaria can easily be distinguished from the more delicate *C. salicornioides* " var. *normani* " by eye. Much of the material consists of isolated internodes, but some complete colonies are present in the specimens from Senegal in the Marche–Marchad Collection. The early stages arise from Hydroid stems, or are attached by rootlets to small conglomerate masses of sand grains, shell fragments and Foraminifera. Frequently the older, dead parts of the colonies have been colonized by species of Foraminifera. *Cellaria* appears to be a genus capable of directly colonizing unstable substrates, although it is not exclusively associated with them.

C. forceps Lagaaij (1952 : 53, pl. 4, fig. 6), from the Coralline Crag (Pliocene, Britain), resembles *C. elongatoides*, but has larger avicularia, and a bifid denticle on the proximal side of the ovicellular orifice.

Cellaria atlantida n. sp.[2]

(Text-fig. 5)

HOLOTYPE. Zoologisk Museum, Copenhagen, marked slide, " Atlantide " Stn. 123, 57Ept.

MATERIAL EXAMINED. Copenhagen Museum. " Atlantide ", Stn. 123, 2° 03′ S., 9° 05′ E., 5.iii.46, 50 m., 57E, paratypes.

DIMENSIONS. Lz 0·50–0·58mm, lz 0·23–0·27mm, Lor 0·08–0·09mm, lor 0·1–0·12mm (Ovicelled zooids Lz 0·49–0·53, lz 0·25–0·29, lov 0·09–0·10mm), Lav 0·55–0·60mm, lav 0·28–0·30mm, Lm 0·23–0·27mm, lm 0·18–0·20mm, Av. L. internode 9 mm.

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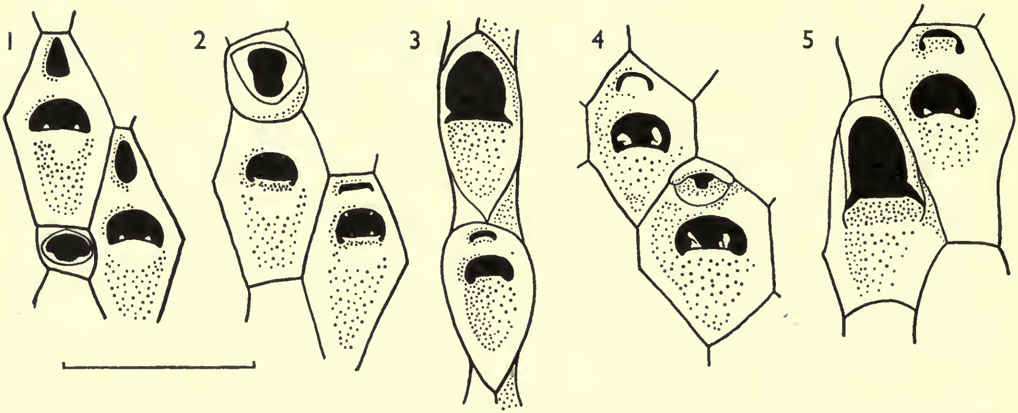
[2] Named after the yacht " Atlantide ", in which the specimens were collected.

Zoarial internodes occasionally long (longest observed, 18 mm.), but not curved. Chitinous joints tubular. Orifices curved proximally, with paired denticles. Ovicellular orifices with a very large proximal denticle. Avicularia as large as the zooids, occasionally larger. Rostrum elongated, rounded distally, not raised. Avicularian cryptocyst extensive. Mandible rounded distally, directed distally.

C. atlantida resembles *C. salicornioides* in its large avicularia, but differs in its denticulate orifice and ovicellular orifice, which are somewhat similar to those of *C. elongatoides*. Like *C. elongatoides*, *C. atlantida* is a robust species, the fertile parts of the internodes reaching 1 mm. in diameter.

C. elongata Canu (1908 : 267, pl. 4, fig. 5, Patagonian, Argentina), resembles *C. atlantida*, but differs from it in its lack of avicularian cryptocyst and its smaller dimensions (Lz 0·38–0·42 mm., lz 0·19–0·21 mm., Lor 0·06 mm., lor 0·09 mm.).



FIGS. 1–5. *Cellaria*. Scale = 0·5 mm. 1. *C. fistulosa* auctt. (non Linnaeus). Off Tangier, 1903. 4. 29. 16pt. 2 zooids with ovicells, and 1 avicularium. 2. *C. sinuosa* (Hassall). Off Tangier, 1903. 4. 29. 10 B. 2 zooids, 1 with an ovicell, and 1 avicularium. 3. *C. salicornioides* "var. *normani*" Hastings. Gulf of Guinea, 1964, Redier Coll. 1 zooid with ovicell and 1 avicularium. 4. *C. elongatoides* Bassler. Marche–Marchad Coll. II. Senegal, 4A. 2 zooids, one with an ovicell, and 1 avicularium. 5. *C. atlantida* n. sp. 1 zooid with an ovicell, and 1 avicularium.

The avicularian cryptocyst appears to become secondarily calcified in some cases, extending almost to the distal end of the rostrum. The mandible is still present.

Most of the colonies from Stn. 123 were young, but nearly all had ovicelled zooids. One zoarium arose from rootlets attached to a lamellibranch shell.

Division **CRIBRIMORPHA** Lang

MEMBRANIPORELLA Smitt, 1873

Zooids with a frontal shield formed of overarching spines which fuse leaving lacunae between them. Ovicell hyperstomial, closed by the operculum.

Membraniporella is here included in the Cribrimorpha purely for convenience.

A summary of the discussions relating to its systematic position has recently been given by Bobin & Prenant (1965 : 289), see also Prenant & Bobin (1966 : 568).

The range of variation of species assigned to this genus is large. It is possible that the similarities of character of the species included are only superficial; but they are here retained in the genus until work can be done on the early astogeny, and on the development of the spines, ovicells and avicularia.

The type-species, *M. nitida*, possesses diatellae; all other species listed here have septulae. It is not known at present whether this is a significant character, as, for example, forms with and without diatellae are known in the Ascophoran genus *Fenestrulina* (see Hastings, 1932 : 427).

Avicularia are present in *M. nitida* and *M. agassizii*, but they are not found in the other species.

The frontal shield of spines may show great inter- and intraspecific variation. In *M. nitida* (notably in some zooids of the type-specimens), the spines may be few in number, with large lacunae. The appearance of these zooids is then similar to those of *M. aragoi* s.s., other zooids are almost indistinguishable from those of *M. distans*. In both these cases, however, specimens of these species may be distinguished from *M. nitida* by the possession of septulae, and by the form of the ovicell.

The following species may be assigned to *Membraniporella*:—

Membranipora agassizii Smitt, 1873 : 11. pl. 5, figs. 103–106, Cuba. Erect, avicularia present, spines little branched.

Membraniporella antarctica Kluge, 1914 : 677, pl. 33, fig. 7, Antarctic. Encrusting, septulae present, avicularia absent, spines little branched.

Flustra aragoi Audouin, 1826 : 240, pl. 10, fig. 1, ?Red Sea, East Indies, Florida. Encrusting, septulae present, avicularia absent, spines little branched.

Membraniporella aragoi var. *pacifica* Osburn, 1950 : 174, pl. 27, figs. 3, 4, Gulf of California to Galapagos. Avicularia absent, spines unbranched.

Membraniporella distans MacGillivray, 1883 : 130, pl. 1, figs. 5, 5a, 5b. Port Phillip Heads, Australia. Encrusting, septulae present, avicularia absent, spines little branched.

Membraniporella magnifica Thornely, 1912 : 144, pl. 8, fig. 5, Cargados, Indian Ocean. Encrusting, opercula thickened and elongated, septulae present, avicularia absent, spines well-branched.

Lepralia nitida Johnston, 1838 : 277, pl. 34, fig. 7, S.W. coasts of Britain and France, Mediterranean, west Africa. Encrusting, diatellae present, avicularia present, spines little branched.

Membraniporella petasus Canu & Bassler, 1928*a* : 36, pl. 4, figs. 1, 2, Cuba. Encrusting, avicularia absent, spines branched and fused so that the frontal shield appears porous in the centre.

Membraniporella pulchra Osburn, 1950 : 176, pl. 27, figs. 5, 6, west Mexico. Encrusting, avicularia absent, spines numerous, unbranched, central area with irregular lacunae.

The following species have in the past been assigned to *Membraniporella*, but are probably referable to other genera:—

Cribrilina alcicornis Jullien, 1883 : 12, pl. 14, figs. 23–25.
Membraniporella baueri Soule, 1959 : 45, text-fig. 5.
Membraniporella corbicula O'Donoghue & O'Donoghue, 1923 : 172, pl. 3, fig. 20.
Membraniporella crassicosta Hincks 1888 : 216, pl. 14, fig. 5.
Lepralia sceletos Busk, 1858 : 262, pl. 20, fig. 3.

Membraniporella nitida (Johnston)

Membraniporella nitida var. *intermedia* Norman, 1909 : 288, pl. 36, fig. 7, Madeira.
Membraniporella nitida (Johnston) Bobin & Prenant, 1965 : 277, Text-figs. 1, I, II; 2, I, I¹; 3, I–III; 4, I, II; 5, I–III; 6, I, II; 7, I, II, VI, Roscoff, France.

MATERIAL EXAMINED. British Museum. Great Britain, Berwick Bay, 1847. 9. 16. 66 pt. (type-material), 1847. 9. 16. 51 (fig'd Busk, 1854, pl. 76, fig. 1), Johnston Coll. Channel Islands, 1963. 3. 30. 132, Harmer Coll. Madeira, 1911. 10. 1. 611 and 660 (type-material of *M. nitida* var. *intermedia*), 1879. 5. 26. 16, Watson Coll. Guernsey, 1919. 6. 24.24, Norman Coll., and many other specimens.

M. nitida does not occur in the west African Collections.

DIMENSIONS. Lz 0·32–0·51 mm., lz 0·29–0·37 mm., Lav 0·13–0·16 mm., Lm 0·08–0·10 mm., Lov 0·15–0·20 mm., lov 0·19–0·25 mm.

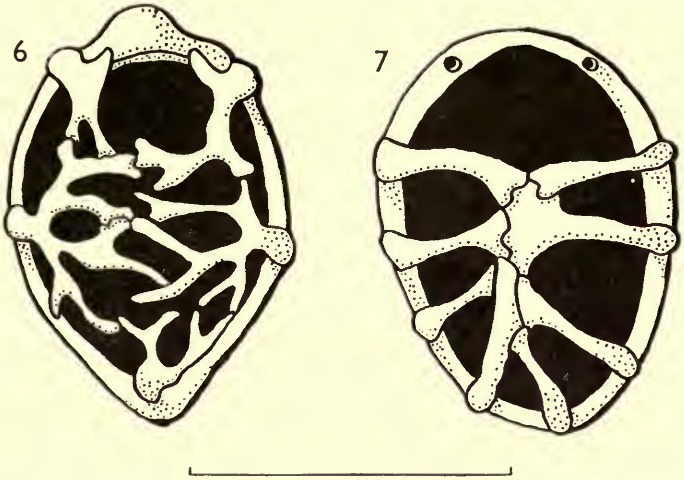
Membraniporella with the frontal shield formed by 8–20 spines, each slightly branched and fused at the tips. Diatellae present. Two pairs of oral spines, present, unbranched. Avicularia present, mandible acute.

The ancestrula (seen in 1963. 3. 30. 132) is membraniporan, with 10–12 long, slightly curved spines, which are not fused at the tip.

The avicularian chambers do not reach the basal lamina, although frontally they appear to occur between the zooids. The chambers are not associated with the dietellae in position (seen in Guernsey, 1919. 6. 24.24, Norman Coll.).

The type-specimen (encrusting shell) has 10–12 wide frontal spines, little branched at the tip, with a wide central area of fusion. Avicularia are rare and small, ovicells plentiful. Busk's figured specimen has longer zooids, but is otherwise very similar. The characters of *M. nitida* var. *intermedia* are not sufficiently distinct or consistent even to rank as varietal. Avicularia are more common, and slightly larger than in the type specimen. In some zooids, as in the type, the number of frontal spines is reduced, and the lacunae between them is correspondingly wider; but in the same colony zooids may be found with numerous frontal spines.

Bobin & Prenant (1965) described an interesting convergence of characters in *Membraniporella* and *Callopora*, an Anascan genus. The species they defined and distinguished, *M. nitida* and *C. rylandi*, both had similar frontal spines, diatellae and avicularia, but differed in the relationships of the ovicell and operculum. *C. rylandi* was described from Roscoff, and there are specimens of the species, from the Channel Islands, which had previously been assigned by Hincks and Norman to *M. nitida*, in the British Museum. All the material from Madeira is referable to *M. nitida*, and the distribution of *C. rylandi* does not apparently extend as far to the south as west Africa. Another species of *Callopora*, which also resembles *Membraniporella*, does, however, occur from this area (see Cook, 1968, in press).



FIGS. 6, 7. *Membraniporella*. Scale = 0·5 mm. 6. *M. marcusi*, n. sp. Achimota Coll., Ghana, 59H. Zooid with ovicell, showing the formation of the frontal shield by the paired distal, and 2 lateral and 1 proximal branched spines. 7. *M. aragoi* (Audouin), Maturo Coll., Florida, 1965. 8. 6. 2. Zooid, showing the formation of the frontal shield by 8 little-branched spines.

Membraniporella marcusi[3] n. sp.

(Plate 1, fig B, Text. fig. 6)

Membraniporella aragoi (Audouin) Marcus, 1938 : 30, pl. 6, fig. 16, Santos, 20 m., Brazil (not *Flustra aragoi* Audouin 1826 : 240, see below).

HOLOTYPE: B. M. Achimota Coll., 59H, figured specimen.

MATERIAL EXAMINED. " Calypso " Coll. II. Stn. 75, 16° 04′ 20″ N., 22° 58′ 10″ W., 25.xi.59, 45 m., C106B, on gorgonid stem.

Achimota Coll. Stn. 35, Dredge 1, 21.xii.50, 37 m., 59H; Stn. 45, Dredge 1, 31.xii.50 m., 62A; Stn. 47, Dredge 1, 4.i.51, 44 m., 14L; Stn. 48, Dredge 2, 4.i.51, 44 m., 46B; Stn. 72, Dredge 3, 24.i.51, 38 m., 61A; Stn. 110, Trawl 1, 4.iv.51, 110 m., 48B; Stn. 111, Trawl 2, 4.iv.51, 43 m., 49L; Stn. 112, Trawl 3, 4.iv.51, 43 m., 60D; Stn. 131, Trawl 1, 2.v.51, 37 m., 41C, 43C; Stn. 132, Trawl 2, 2.v.51, 44 m., 40N, 42B; Stn. 133, Trawl 2, 2.v.51, 51 m., 45B; all on *Jullienella foetida.*

" Atlantide " Coll. Copenhagen Museum. Stn. 44, 10° 22′ N., 16° 22′ W., 17.xii.45, 41–55 m., sand and shell, 63C, on *Cupuladria canariensis*. Stn. 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m., stones, 45P, on *Discoporella umbellata.*

M. marcusi is not present in Marche–Marchad Collection.

DIMENSIONS. Lz 0·45–0·67 mm., lz 0·40–0·52 mm., Lov 0·10–0·17 mm.

Zoarium encrusting. Zooids with cryptocyst and gymnocyst small. Frontal shield formed by the fusion of the tips part of the paired oral spines and of 3–5 irregularly and profusely branched spines occurring round the opesia. One pair of branched oral spines, part of which are fused with the lateral walls of the ovicell, when present. Ovicell small, shallow, with a raised frontal protuberance.

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[3] Named after Professor Ernst Marcus, who first described this species.

The ancestrula, like that figured by Savigny for *M. aragoi* (see below), is membraniporan, with 4–6 simple marginal spines, which are not fused at the tip. The average Lan is 0·25 mm.

Membraniporella marcusi has many features in common with *M. aragoi*, but differs entirely in the number and form of the spines. Although Savigny's excellent figures makes recognition of *M. aragoi* easy, no material from the type-locality is available, and, in view of the variation of character within *Membraniporella*, and the apparent close convergence of the genus with *Callopora*, it is unfortunate that certain details of the structure of *M. aragoi* are unknown. For example, specimens assigned to *M. aragoi* from other areas (see below) have septulae, but, as noted above, zooids of *M. nitida* and *M. distans* may appear identical, in the absence of other distinguishing characters, yet one has dietellae, the other, septulae.

Waters (1909 : 167) recorded *M. aragoi* from the Red Sea, and it may be presumed that this is the type-locality. Recent collections made there by the author, and by others, have unfortunately failed to provide any specimens. Harmer (1926 : 473) reported *M. aragoi* from the East Indies, and his figure is very similar to Savigny's. Kluge (1955 : 106) recorded it from Japan. It must be assumed that these forms are the same as that mentioned as occurring in the Caribbean by Osburn (1950 : 175). The British Museum does possess a specimen from Florida (1965. 8. 6. 2, Maturo Coll)., which is also very similar in character to Savigny's figure. The zooids have 6–8 regular, little-branched spines round the opesia, and the branched oral spines are fused with the proximal part of the lateral walls of the ovicell as in Savigny's figure 1^3. This type of fusion also occurs in *M. marcusi* and *M. magnifica*. Septulae are present in the Floridan specimen. The zooids are, on average slightly smaller than those of *M. marcusi*.

Both the west African specimens of *M. marcusi* and Marcus's figure differ from *M. aragoi* in the smaller number of spines round the opesia. There are usually 4, but occasionally 5 are present. These spines are profusely branched, spines of the 3rd and occasionally the 4th order occurring, (compare Text-figs. 6, 7). In all the plentiful material from west Africa, there is no tendency towards production of a frontal shield of simple little-branched spines, as in *M. aragoi*. Some scattered zooids do, however, have only 3–4 short, simple, curved spines, which do not fuse at the tip, which appears to be a reversion to the ancestrular condition. The west African material differs from the Brazilian only in the rarity of occurrence of the single distal spine figured by Marcus.

The development of the spinous processes across the frontal membrane in *M. marcusi* shows some similarities to that seen in *Cribrilina punctata* (see below). The distal pair of spines appears to grow at the same rate as the more proximal spines, and does not fuse first (cf. *Cribrilaria radiata*, p. 333). The distal 1st and 2nd order branches of the oral spines are free, and either directed upward, or fused with the lateral walls of the ovicell, if present. The most proximal 2nd order branches of the oral spines fuse first with their most distal counterparts of the nearest opesial spines. They then continue to grow across the frontal membrane and fuse centrally, forming the equivalent of an apertural bar. In *M. aragoi* the bar is formed entirely by the distal pair of opesial spines, not by part of the oral spines.

The Achimota Collection specimens of *M. marcusi* all encrust the arenaceous test of the Foraminiferan, *Jullienella foetida* Schlumberger (see Nørvang, 1961, and p. 348). This appears to be one of the principal substrates available for encrusting Polyzoa, which are otherwise unable to settle on the muddy sea-bottom of the Gulf of Guinea (see Buchanan, 1958 and Bassindale 1961). It is interesting that the specimens from further North, where *Jullienella* may be less common (see Cook, 1964*b* : 73), have colonized specimens of species of Cupuladriidae, which are almost exclusively associated with sandy and muddy sea-bottoms. Osburn (1950 : 176) noted that his specimens of *M. pulchra* exclusively encrusted the basal side of specimens of *Cupuladria*.

CRIBRILARIA Canu & Bassler

Cribrilaria Canu & Bassler, 1928*b* : 27, footnote.

The genus has been discussed by Canu & Bassler (1929*a* : 33) and by Lagaaij (1952 : 57).

Cribrilaria radiata (Moll)

Colletosia radiata (Moll) Harmer, 1926 : 475, pl. 34, figs. 15–18, East Indies.
Cribrilaria radiata (Moll) Lagaaij, 1952 : 57, pl. 4, fig. 9, Tertiary, Europe.

MATERIAL EXAMINED. " Calypso " Coll. I. Stn. 17, 5° N., 5° 28′ 30″ W., 21.v.56, 27 m., C56D, on *Jullienella*. Stn. 110, Grand Frère N.E., 1° 2′ 45″ N., 7° 17′ 37″ E., 7.vii.56, 25–40 m., C9E, on stone with *Callopora* sp.; Coll. II. Stn. 14, 14° 53′ 43″ N., 23° 31′ 24″ W., 17.xi.59, 25–30 m., C68H; Stn. 31, 14° 53′ 55″ N, 23° 29′ 58″ W., 19.xi.59, 75–170 m., C66J, with *Crepidacantha setigera*; Stn. 42, Punto do Anciao, 20.xi.59, 15–30 and 60 m., C104B, on shell; Stn. 75, 16° 04′ 20″ N., 22° 58′ 10″ W., 25.xi.59, 45 m., C117B.

Marche–Marchad Coll. I. 4E, Cap Matakong, Guinée Ise, on shell with many other species. Coll. II. 31E., S.W. Ise de Madeleines, 9.i.54, 47·5 m., on bivalve shell.

Achimota Coll. Stn. 126, Trawl 3, 12.iv.51, 20 m., 37 I.

Copenhagen Museum. Las Palmas, 150–160 m., 74B. La Luz, Gran Canaria, 15–20 fath., 88E; 100 fath., 89G. Mortensen Coll. " Galathea " Stn. 4, 22° 19′ N., 17° 05′ W., 2.xi.50, 62 m., 80E.

" Atlantide " Stn. 44, 10° 22′ N., 16° 22′ W., 17.xii.45, 41–55 m., 63E. Stn. 45, 9° 23′ N., 15° 07′ W., 18.xii.45, 30–36 m., 78E. Stn. 145, 9° 20′ N., 14° 15′ W., 13.iv.46, 32 m., 7B, 110N. Stn. 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m., 45E, 107H, 116A.

British Museum. Madeira, 1899. 7. 1. 1348, 1354, 1355, 4725, Busk Coll.; 1899. 5. 1. 721, Hincks Coll; Port of Oratava, Canary Is., 50 fath., 1899. 7. 1. 1350, Busk Coll.; Tangier, 1899. 7. 1. 1356, 1357, 1360, Busk Coll.; Gulf of Mexico, 28° 58′ N., 89° 9′ W., South Pass of Mississippi River, 1961. 11. 2. 39, Cheetham Coll.

DIMENSIONS. Lz 0·49–0·60 mm., lz 0·23–0·45, Lor 0·05–0·07 mm., lor 0·07–0·09 mm., Lov 0·13–0·19 mm., lov 0·17–0·20 mm., Lav 0·21–0·32 mm., Lm 0·17–0·27 mm.

Zoarium encrusting. Frontal shield of zooids formed by 10–24 costae. 5–7 oral spines. Avicularia vicarious, between the zooids, chambers reaching the basal lamina, mandibles acute, often elongated. Ovicells small, imperforate, slightly raised in the centre. Diatellae present. Ancestrula membraniporan.

The range of variation of this wide-spread form has been fully discussed by Harmer (1926 : 475–8). It has been reported from Madeira by several authors. The west African form shows the small, raised bosses or papillae at the bases of the costae, and the avicularia frequently have greatly elongated mandibles, and raised rostra. *C. radiata* occurs on shell, stone, and *Jullienella*.

The development of the frontal shield shows interesting similarities with that of some specimens of *Triporula* (see below).

Division **ASCOPHORA IMPERFECTA** Harmer

Ascophora Imperfecta Harmer, 1957 : 645.

Harmer defined the Ascophora Imperfecta to include those genera in which the frontal membrane and contiguous operculum were covered by an overarching frontal shield. A true compensation sac, developing from a group of cells at the proximal edge of the operculum, is therefore not developed.

Two distinct methods of formation of the frontal shield appear to be present in the species referred here to the Ascophora Imperfecta. One type is that already described by Harmer. The frontal shield develops as a curved lamina, with its concavity directed proximally, which grows over the frontal membrane in a distal direction. Genera with this type of frontal shield are here represented by species of *Hippopetraliella* and *Metrarabdotos*. In the second type of development a pair of distal processes first fuses centrally to form a bar which delineates the orifice proximally. An irregular series of flattened, rounded processes then develops across the frontal from the lateral and proximal walls of the zooid. These processes later fuse, leaving large foramina which then calcify further. This type of development has only recently been observed. It is known to occur at present in three genera; *Tremogasterina* (see Powell & Cook, 1967), *Exechonella* and *Triporula* (see below). Further observations will almost certainly show that other genera have a similar type of development, and probably that still other, differing, types of frontal structure are present in the Ascophora Imperfecta.

The second type of development resembles that seen in two species of Cribimorph, *Cribrilaria radiata* and *Cribrilina punctata*. In *C. radiata* the distal pair of costae fuse first, forming the apertural bar which delimits the proximal edge of the orifice. On the proximal side of these costae, lacunae are left uncalcified where the fusion is incomplete (see Harmer, 1926 : 477). The remaining costae advance across the frontal membrane as a series of hollow, flattened spinous processes, which form cross connections, producing the rows of intercostal lacunae. This development is superficially similar to that seen in some specimens of *Triporula stellata* (see p. 342). In *Cribrilina punctata* the development is of a slightly different nature. A pair of distal spines develop, but does not always fuse first. Simultaneously other irregular spinous processes arise round the gymnocyst. In the material examined, the order and position of the fusions of these processes seem to have a fairly constant pattern (see Text-fig. 11). The resulting foramina are large, and at first, irregular. Later calcification produces the regularly porous frontal shield characteristic of the species. This type of development resembles both that of *M. marcusi* (see above), and that of *Exechonella tuberculata* (see below).

Some of the developmental stages described by Larwood (1962 : 25–32) in the Cribrimorpha differ from those described above. Before any analogies and homologies can be established, much further work must be done on the development of living colonies of a large number of genera (see Osburn, 1940 : 366, 368).

It is interesting to note, however, that Waters (1923 : 548–9) described apparent lateral processes involved in the calcification of the frontal wall of the Ascophoran, *Lepralia otto-mulleriana* Moll (see also Larwood, 1962 : 28). A specimen, labelled *L. otto-mulleriana* by Waters, and sent by him to O'Donoghue, has recently been incorporated into the British Museum from the O'Donoghue Collection. It is from Santa Margharita; the material described by Waters in 1923, was from Mentone. Unfortunately, the specimen was preserved dry, but restoration with 10% solution of trisodium phosphate revealed the following features. The primary frontal wall is very thinly calcified. It appears to be developed from a series of broad plates, a distinct central suture, with 3–4 lateral sutures extending from the margins of the zooids, and alternating with the marginal pores, being visible. Occasional small pores occur on the suture lines, where the plates have joined incompletely. The secondary calcification extends from around the marginal pores, and does not obscure the central pores. If a suboral avicularium is developed, its chamber is formed by secondary calcification.

The specimen is now preserved in alcohol (registration number 1966. 9. 2. 3.).

It is not yet known how much importance may be attached to the type of ancestrula found in Polyzoa, or how much inter- and intraspecific variation may occur. The ancestrulae of *Membraniporella*, *Cribrilaria radiata* and *Cribrilina punctata* are membraniporan (see above), as is that of *Tremogasterina*. That of *Hiantopora bidenticulata* Canu & Bassler, which is here provisionally associated with *Triporula*, is cribriform (see below). A similar ancestrula was described for the otherwise apparently Ascophoran species, *Temachia opulenta*, by Jullien (1883 : 509, pl. 14, figs. 26–29), and for *Schizoporella küensis* Okada & Mawatari, by Mawatari (1952 : 279, text-fig. 13). The ancestrulae of *Exechonella* and *Triporula* however, are smaller than, but are essentially of the same character as later developed zooids.

TREMOGASTERINA Canu

Tremogasterina Canu, Powell & Cook, 1967.

Zoarium encrusting. Zooids with a frontal shield formed by the coalescence of marginal processes, leaving large foramina. Orifice contracted laterally, with oral spines. Ovicells hyperstomial. Avicularia usually present. Diatellae and septulae present.

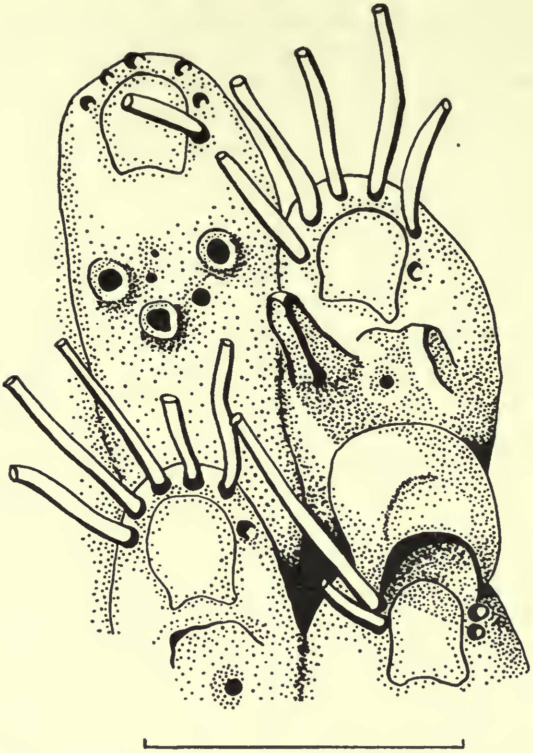

FIG. 8. *Tremogasterina*. Scale = 0·5 mm. *T. perplexa* n. sp. " Atlantide " Coll., Stn. 146, off French Guinea, 107F. 4 zooids, 1 with an ovicell. Note the large, tubular frontal foramina, and the irregular growth of the tuberculate frontal processes.

Tremogasterina perplexa[4] n. sp.

(Text-fig. 8)

HOLOTYPE (and only specimen):—" Atlantide ", Stn. 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m., 107F. Copenhagen Museum.

DIMENSIONS. L z 0·42–0·65 mm., l z 0·35–0·42 mm., Lor 0·12–0·14 mm., lor 0·11–0·13 mm. L_{spine} 0·25–0·42 mm.

Tremogasterina with no avicularia. Zooids separated by deep grooves. Orifices elongated, with the proximal border curved distally. Six large oral spines present. Frontal shield smooth, with a central area perforated by 5–9 lunate foramina. Two distal diatellae, and 2–4 lateral septulae. Ovicells with a frontal area.

In spite of the complete absence of avicularia, the affinities of this species are with *Tremogasterina*. The zooids resemble the periancestrular zooids of *T. robusta* (Hincks), and the zooids of *T. spathulata* (Canu & Bassler) (see Powell & Cook, 1967), in the small cribriform central area of the frontal shield. The form of the orifice, the oral spines, the ovicell, diatellae and septulae are all characteristic of the genus.

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[4] Latin, *perplexus*, involved, referring to the difficulties in assigning secondarily calcified zooids to the genus *Tremogasterina*.

The colony comprises approximately 75 zooids, and encrusts the surface of a dead colony of *Membranipora arborescens* (Canu & Bassler), which itself grows over an echinoderm test. At the growing edge a few zooids show that the frontal shield develops from a series of coalescing, spinous processes, as in the other species of the genus. The oral spines are large, and very long; the most proximal pair frequently being the stoutest. A pair of small distal diatellae, and 2–4 lateral septulae are present. The orifice is elongate like that of *T. robusta*; the opercula are dark brown, and appear to have a marginal sclerite. The proximal border of the orifice is curved distally.

Secondary calcification greatly alters the appearance of the zooids. The foramina become surrounded by short tubular extensions, similar to those found in *Exechonella tuberculata* (MacGillivray). The distal part of the frontal shield, or apertural bar, becomes enormously thickened; a high, ridged mucro sometimes developing, which may obscure the orifice and eventually the frontal foramina. The spines are present in nearly all the zooids. One ovicell is present, it has a small frontal area.

EXECHONELLA Canu & Bassler

Exechonella Canu & Bassler, 1927 : 4. Harmer, 1957 : 652.

Zoarium encrusting. Zooids large. Frontal shield with numerous large foramina. Avicularia present or absent.

Avicularia have been recorded in *E. magna*, *E. antillea* and *E. pumicosa*, but their occurrence in the last two forms is apparently sporadic (see below). Ovicells have been reported in one species, *E. discoidea* Canu & Bassler (1929*b* : 123).

Lagenipora tubulosa d'Orbigny, described by Canu (1909 : 450, pl. 12, fig. 11), from the Burdigalian of Dax, France, belongs to *Exechonella*.

The zoaria of *E. antillea* in these Collections are nearly all slightly worn, and well-preserved growing edges are not present. A few zooids, particularly one in specimen Achimota 65C, show evidence that the frontal shield has been formed by the fusion of irregular processes. The development of the frontal shield in *Exechonella* has, however, been seen particularly clearly in specimens of *E. tuberculata* (MacGillivray) from Port Phillip Heads, Australia (1897. 5. 1. 930, 931, J. Bracebridge Wilson Coll.). The proximal part of the orifice is formed by the central fusion of the 2 most distal of a series of irregular lateral and proximal processes (see Text-figs. 9, 10). The processes fuse, forming large foramina, which then calcify further, forming tubular processes in this species.

Exechonella antillea (Osburn)

(Plate 1, fig. E)

Lepralia antillea Osburn, 1927 : 6, text-fig. 6, Curaçao on shell, pottery.

Exechonella pumicosa Canu & Bassler, 1928*a* : 70, pl. 14, fig. 1, text-fig. 11a, South of Florida, 40 fath., on shell.

Exechonella antillea (Osburn) Osburn, 1940 : 366, Porto Rico, on rock and shell. 5–20 fath; 1950 : 95, pl. 10, figs. 9, 10, Gulf of California; Shier, 1964 : 616, N.W. Florida, on rock and shell.

?*Exechonella brasiliensis* Canu & Bassler, 1928c : 72, pl. 3, fig. 5, Brazil.

Exechonella sp. (18.A from Ghardaqa); Harmer, 1957 : 653.

MATERIAL EXAMINED. " Calypso " Coll. I. Stn. P21, Entre Pt2 da Mina et Ise S. Ana, 4.vii.56, 8–10 m., C8E; Stn. 110, Grand Frère, N.E., 1° 20′ 45″ N., 7° 17′ 37″ E., 7.viii.56, 5–46 m.

Achimota Coll. Stn. V, Tenpobo ¼ m. square section on rock, 5.ii.50, 8B, C, 65C, Coll. II, 17B; Stn. 69, Dredge 5, 22.i.51, 22 m., 90G.

Copenhagen Museum " Atlantide " Coll. Stn. 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m., 107V.

British Museum, Ghardaqa, Red Sea (18A), 1961.10.30.3. Aden, Khormaksar sands, on shell, 1965. 9. 4. 2, Sgt. Cambridge Coll. St. Thomas, W. Indies, 1887. 8. 1. 1–3, " Challenger " Coll.

E. antillea is not present in the Marche–Marchad Collection.

DIMENSIONS. Lz 0·70–0·95 mm., lz 0·60–0·80 mm., Lor 0·20–0·23 mm., lor 0·24–0·26 mm. Lav 0·07–0·10 mm., Lm 0·03–0·06 mm. 15–40 foramina, av. width 0·025 mm.

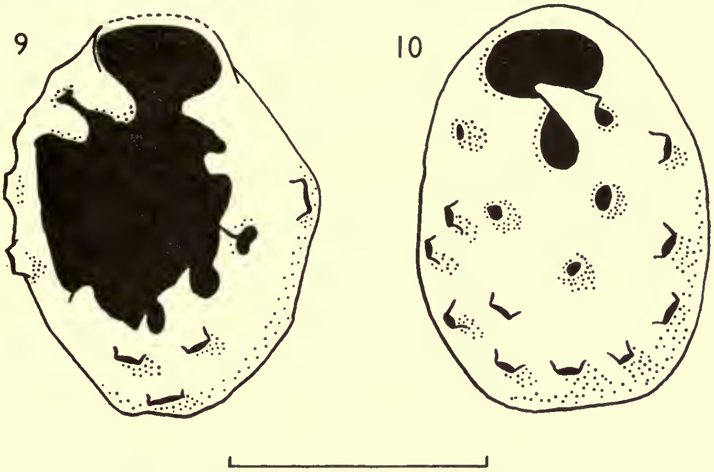
Zooids large, very irregular in shape, separated by deep grooves. Operculum dark, with marginal and proximal sclerites. Orifice with raised, flaring peristome, sometimes with spinous processes. Frontal foramina round, regular, funnel-shaped, surrounded by a salient rim when fully developed. Avicularia very rare, minute, developed from a foramen, mandible rounded.

The range of variation of all characters in this species is large. The zooids vary greatly in size, those near the ancestrula being very small. The later-developed zooids are large, and very irregular in shape. The shape of the orifice may be wider than long, or longer than wide. The position of the oral condyles varies from half, to two thirds of the way down the orifice from its distal border. The size and direction of the condyles also varies. In the " Atlantide " material they are large, and point inward across the orifice. In the Achimota specimens the condyles are smaller, and point downward into the cavity of the zooids. The frontal foramina, when fully developed, are surrounded by salient rims, which are funnel-shaped. The number of pores is directly related to the size of the zooids, and ranges from 15–40.

The zoaria encrust shell and stone, and the older, dead parts of colonies of *Steganoporella magnilabris*. The peristomes often show signs of wear, but some zooids, growing in the hollows of shell etc., notably those from Achimota Stn. 69, and " Atlantide " Stn. 146, have well raised distal and lateral flaring expansions. Four zooids in the Achimota specimen also have a short spike-like protuberance on the proximal side of the orifice. The " Atlantide " specimen has zooids with long spinous processes arising from the edge of the peristomes.

Minute avicularia are present in the material from the West Indies and the " Atlantide " Collection. They appear to be derived from one of the lateral frontal foramina, and are usually found at the lateral borders of the zooids (see Osburn, 1927 and 1940). The subrostral chamber is raised, sometimes tubular. The avicularian mandible is short and rounded, and is variously orientated. Minute avicularia are also very occasionally present in the colonies from the Red Sea, which agree in all characters with those from West Africa. Osburn specified the presence of avicularia in *E. antillea*, and they were described by Canu and Bassler in *E. pumicosa*. Avicularia are not always present and are usually absent from large areas of the colony. Osburn (1950) did not mention their occurrence in his California material.

Osburn considered that *E. pumicosa* (Canu & Bassler) was a synonym of *E. antillea*. *E. brasiliensis* (Canu & Bassler) was also described with small avicularia, but the number of frontal foramina was very small (13–15). In all other respects *E. brasiliensis* greatly resembles *E. antillea* and is certainly a closely related form; the discovery of further material may show that it is synonymous with *E. antillea*.



FIGS. 9, 10. Development of the frontal shield in *Exechonella*. Scale = 0·5 mm. 9. *E. tuberculata* (MacGillivray). Port Phillip Heads, 1897. 5. 1. 930. Zooid at the growing edge, showing formation of the apertural bar and frontal foramina, which rapidly become calcified to form tubular processes. 10. *E. tuberculata*. Port Phillip Heads, 1897. 5. 1. 931. Zooid at a later stage of development, showing closure of the apertural bar.

Exechonella gigantea n. sp.[5]

(Plate 2, figs. C, D)

HOLOTYPE (and only specimen), B. M. Sud de Gorée, 24. 11. 53, 4–41 m., 11J, Marche-Marchad Coll. I.

DIMENSIONS. Lz 1·20–1·60 mm., lz 0·90–1·40 mm., Lan 1 mm., Lor 0·20–0·26 mm., lor 0·20–0·26 mm. 60–80 frontal foramina, average width 0·02 mm.

Zoarium encrusting. Zooids extremely large. Orifices with a thickened peristome, raised laterally and distally. Operculum with a marginal sclerite and thickened rim. Avicularia and ovicells not seen.

The zoarium completely covers one valve of a small lamellibranch shell 10 mm. in diameter, and comprises approximately 200 zooids. The ancestrula is smaller than, but has the same characters as the later developed zooids. The zooids on the convex (and presumably exposed) side of the shell have low, thickened peristomes. The peristomes of those in the concavity have raised, flaring expansions, which tend to be bifid distally (see pl. 2, fig. D).

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[5] Latin, *giganteus*, large, referring to the size of the zooids.

Although the zooidal characters of *E. gigantea* are very similar to those of *E. antillea*, the size of the zooids, which shows no intergrading, appears to exclude it from that species. *Cyclicopora grandis* Duvergier (1921 : 174, pl. 2, figs. 2, 3), from the Lower Miocene of Bordeaux, is very similar to *E. gigantea* in all characters, and is certainly referable to *Exechonella*. The zooids are slightly smaller, and the orifices have distinct oral condyles, which are absent in *E. gigantea*. Duvergier also recorded that avicularia were present in *C. grandis* but in view of the variability of their occurrence in *E. antillea*, this is probably not a difference of any specific value.

The discovery of further material of *E. gigantea*, may show that it may be referred to *E. antillea*, but the present specimen appears to be distinct from that species.

TRIPORULA Canu & Bassler

Triporula Canu & Bassler, 1927 : 8.
Enantiosula Canu & Bassler, 1930 : 23.

TYPE-SPECIES, *Escharipora stellata* Smitt, 1873.

Zoarium encrusting. Zooids with a frontal shield pierced by stellate pores formed from irregular foramina. Diatellae present. Paired lateral avicularia (not replacing diatellae) present, bar absent. Ovicells not known.

Smitt (1873 : 24–6) included *Escharipora* (?) *mucronata* as the first species, with *E. stellata*, and also suggested that *Eschara lichenoides* Busk, 1854 (= *Adeonellopsis yarraensis* (Waters) (see Harmer 1957 : 799) and *Lepralia distoma* Busk, 1856 (= *A. distoma*, see Canu & Bassler, 1920 : 564), were congeneric. *E. mucronata* is referable to *Tremogasterina* (see Powell & Cook, 1967 : 9), and *E. stellata* was formally chosen as the type-species of *Triporula* by Canu & Bassler (1927).

Enantiosula, with the type-species *E. manica*, was defined with the frontal " a tremocyst ". Examination of specimens shows that the frontal shield of *E. manica* is of the same nature as that of *T. stellata* and that the two species are not only congeneric but synonymous.

Canu & Bassler (1929*b* : 385) suggested a close relationship between *Triporula* and *Anarthropora* Smitt. Brown (1952 : 357), who examined specimens of both *A. monodon* (Busk), the type-species, and *Triporula biarmata* (Waters) (see below), considered them to be congeneric. Both forms are similar, and the two genera may be placed in the same family. The structure of the frontal shield in *A. monodon* (seen in 1963. 3. 30. 9, Shetland, 80–170 fath., Harmer Coll., 1919. 6. 25. 128, Shetland, Norman Coll., and 1899. 7. 1. 1452, Guernsey, Busk Coll.), shows that it belongs to the Ascophora Imperfecta. It resembles *Triporula* in possessing diatellae, numerous stellate pores, and in the absence of spines and ovicells. It differs in the following important characters, however. The small, distal avicularium is in series with, and replaces, one of the diatellae; there are no lateral avicularia, and the proximal avicularium develops from a fold in the peristome, which is a proximal upward extension of the apertural bar. It therefore seems advisable to maintain the two genera separately.

A. horrida (Kirkpatrick, 1888 : 76, pl. 8, fig. 2, Mauritius) was provisionally referred to *Teuchopora* by Harmer (1957 : 654).

Hiantopora bidenticulata Canu & Bassler (1929*b* : 115, pl. 11, figs. 9–11, Philippines) shows several characters similar to those of *Triporula*. Comparison with specimens of the type-species of *Hiantopora* (*H. ferox* MacGillivray, 1899. 7. 1. 1371, Busk Coll., and 1897. 5. 1. 620, Australia, see Harmer, 1926 : 237), shows that *H. bidenticulata* is not referable to *Hiantopora*. A specimen from Funafuti (60 fath., 1903. 1. 29. 23) has slit-like diatellae, and paired avicularia arising in the same manner as those in *Triporula* (see below). The frontal shield resembles that of *Triporula*, but the foramina are irregular and not stellate. *H. bidenticulata* differs from *Triporula* in possessing distal spinous processes (which are, however, not true spines), on the peristome. There is no distal avicularium or enlarged pore as in *Triporula*. The irregular frontal foramina resemble those of *Tremogasterina spathulata*, see Powell & Cook (1967 : 11), but the avicularia have no bar. Generally, the characters of *H. bidenticulata* are very similar to those of *Triporula*, and until plentiful material allows the complete examination of the species, it may be associated with that genus.

" *Triporula* " *bidenticulata* differs from other known species of *Triporula* in possessing a cribrimorph ancestrula. One is present on the slide from Funafuti. There are 7 costae on each side, and 5 oral spines.

Triporula plana was described (as *Enantiosula*) by Osburn (1952 : 469, pl. 57, figs. 8–9) from Lower California, from 30 fath. It differed from *E. manica* in its smaller lateral avicularia, larger distal avicularium, and smaller zooids.

Triporula biarmata (Waters) was placed in *Anarthropora* by Brown (1952 : 357, see above), who chose the specimen (B. M. Palaeontology Department, D 32974) from Mount Gambier, S. Australia, as lectotype. The zooids of this specimen are small (Lz 0·43–0·52 mm., lz 0·22–0·26 mm.), whereas those of Recent material (1897. 5. 1. 688–692, Port Phillip Heads, Victoria, Bracebridge Wilson Coll.) are considerably larger (Lz 0·75–0·90 mm., lz 0·38–0·44 mm.). Some fossil specimens (e.g. D. 35460 and 34750) also have large zooids, however, as had Waters's figured specimens (see Brown, 1952). The Recent specimens from Port Phillip have ancestrulae; these are smaller than, but resemble the other zooids in all characters.

Some Eocene species from North America are apparently closely related to *Triporula*; all have large frontal pores and lateral oral avicularia.

Cheilopora (?) *labiosa* Ulrich, 1901 : 220, pl. 60, figs. 15, 16, see Canu & Bassler, 1920 : 526, pl. 2, figs. 1–3, Lower Eocene, Maryland. Described with lateral avicularia, ovicells absent.

Meniscopora subplana Ulrich, 1901 : 219, pl. 59, figs. 17–18, see Canu & Bassler, 1920 : 556, pl. 2, figs. 4–5, Lower Eocene, Maryland. Described with plurilaminar zoaria, frontal, marginal and basal pores (?diatellae), and paired avicularia. Ovicells absent, but enlarged " gonoecia " present.

Cheilopora prelucidioides Canu & Bassler, 1920 : 527, pl. 68, figs. 1, 2, Upper Eocene, S. Carolina. Described with lateral avicularia and fusiform diatellae.

Anarthropora (?) *verrucosa* Canu & Bassler, 1920 : 430, pl. 7, fig. 20, Lower Eocene, Georgia. Described with three oral avicularia, ovicells absent.

Phylactella magniporosa Canu (1918 : 306, pl. 9, fig. 7), from the Lutetian (Lower

Eocene) of Aude, France, resembles *Triporula* in the shape of the orifice and porous frontal shield. Ovicells were stated to be present, however, and avicularia were apparently absent.

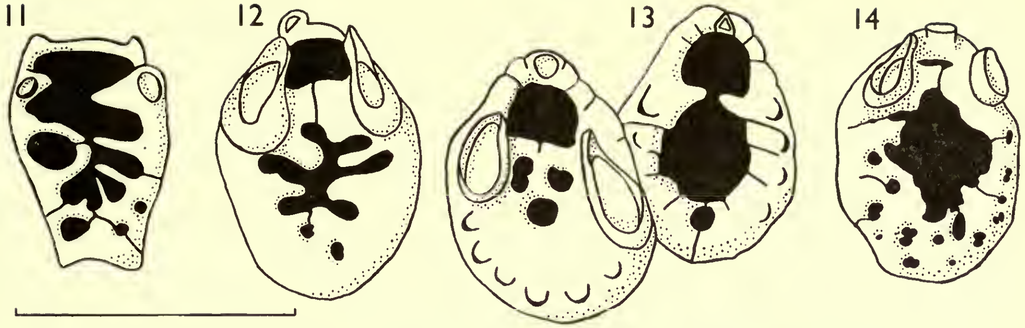
The development of the frontal shield and avicularia in *Triporula* has been seen in *T. stellata* (in both the type specimen and in material from west Africa), and in *T. biarmata* (see below). It resembles that seen in *Tremogasterina* (see Powell and Cook, 1967) and differs from the "umbonuloid" development described for the Ascophora Imperfecta by Harmer (1957).

The future shape of the zooids may be seen at the growing edge of the colony, delineated by the diatellae, which apparently form completely very early in the development of a new zooid. A thin calcified lamina then grows upward above the diatellae, until it is approximately twice their height, the zooids of *Triporula* being very deep. The lamina then curves inward slightly, and a series of ridges develops laterally and distally. These ridges bear no relationship in frequency or position to the diatellae. As the ridges deepen and lengthen, the spaces between them become partially roofed over by calcification above the level of the primary lamina. This produces a series of marginal pores round the entire zooid, which may at first sight be mistaken for diatellae. A lateral pair of these pores remains open, forming the subrostral chambers of the lateral avicularia. The most distal pore may remain open, or may form a distal avicularium. The more proximal pores appear to close, forming a continuous, ridged lamina, round the zooid. In describing *E. manica*, Canu & Bassler (1930 : 24) considered that the avicularia replaced the diatellae. Canu & Bassler's figure (pl. 3, fig. 10) purported to show the avicularia "visible among the diatellae". The distal part of the photograph shows the young zooids with a row of diatellae, all of the same size; no avicularia are visible. The more proximal zooids show the next stage of development. The aperture of the zooids is reduced by the incurving of the lamina, which shows the marginal pores, and the larger, distal lateral pair which will become the subrostral chambers of the avicularia. Unfortunately, the apertures of the pores have been retouched in the photograph. Osburn (1952 : 469) mentioned that the avicularia in *E. manica* were not interzooecial.

The next stage of development may differ slightly in *T. biarmata* from that in *T. stellata*. In *T. biarmata* two free distal processes arise from the lamina and fuse centrally, forming an apertural bar. The lateral and proximal parts of the lamina advance irregularly above the frontal membrane, leaving rounded foramina (see Text-fig. 14). In *T. stellata*, long, free, irregular processes coalesce over the frontal membrane, leaving irregular foramina in some specimens (see Text-fig. 12). In other specimens, the processes appear as flattened spines, and advance regularly across the frontal in a manner very similar to that seen in *Cribrilaria radiata*. In both *T. biarmata* and *T. stellata*, minute spinules growing inward from the edges of the foramina form the stellate pores characteristic of the genus.

The avicularian chambers enlarge and usually obscure the lateral ridges. The aperture lengthens into a tubular peristome and in older zooids, there is a tendency for the frontal pores to become occluded by calcification.

Ancestrulae have been seen in *T. biarmata* and *T. stellata*. They are smaller, and



FIGS. 11–14. Development of the frontal shield in *Cribrilina* and *Triporula*. Scale = 0·5 mm. 11. *Cribrilina punctata* (Hassall). Rasmussen Coll., Fredericksund, Denmark. Zooid from the growing edge, showing the spinous processes anastomosing to form rounded foramina. 12. *Triporula stellata* (Smitt). Redier Coll., Gulf of Guinea, 1964. Zooid showing formation of the apertural bar and anastomosing spinous processes. 13. *T. stellata.* " Calypso " Coll., Stn. 17, C56 I. 2 zooids showing the formation of the apertural bar (on right) and avicularian chambers (on left). 14. *T. biarmata* (Waters). Hincks Coll., Port Phillip Heads, 1899. 5. 1. 690–692. Zooid from the growing edge, showing formation of the apertural bar and frontal foramina.

have fewer frontal pores than the later developed zooids, but are otherwise similar in character.

Ovicells have not been seen in *Triporula*. Enlarged apertures, which may have marked the position of fertile zooids were described in *Adeonellopsis coccinella*, but none have been seen in any of the specimens examined here.

Canu & Bassler (1930 : 24) stressed that the zooids of the superposed layers of colonies of *Enantiosula* grew exactly above the zooids of the lower layer. The edges of the superposed layers are very regular, but the position and orientation of the zooids does not appear to bear any relationship to the underlying layers. The zooecia of the primary layer in *T. stellata* (e.g. " Calypso " C56I), which encrusts stone, appear to be slightly longer, and more irregular in shape, than those of other colonies, which are plurilaminar.

Triporula stellata (Smitt)

(Plate 2, figs. A, B, Text-figs. 12, 13)

Escharipora stellata Smitt, 1873 : 26, pl. 6, figs. 130–133, Florida, 42–183 fath. (not *Escharipora stellata* MacGillivray = *T. biarmata* (Waters), see above).
?*Adeonellopsis coccinella* Canu & Bassler, 1923 : 161, pl. 24, figs. 5–8, Lower Miocene, Florida.
Triporula stellata (Smitt) Canu & Bassler, 1927 : 8.
Enantiosula manica Canu & Bassler, 1930 : 23, pl. 3, figs. 6–11, text figs. 5A–F, Galapagos. Osburn 1925 : 469, pl. 57, Gulf of California to Galapagos.

MATERIAL EXAMINED: Holotype, Naturhistoriska Riksmuseet, Stockholm, No. 1805, Lå 19, 218.

" Calypso " Coll. I, Stn. 1, 21° 05′ N., 17° 14′ W., 10.v.56, 43–45 m., C51A, on coral. Stn. 17, 5° N., 5° 28′ 30″ W., 21.v.56, 27 m., C56I. Stn. 25, 4° 36′ 5″ N., 1° 31″ W., 24.v.56, 50 m., C10Q, on stone. Stn. 107, 1° 26′ 15″ S., 5° 35′ 40″ E., 4.vii.56, 60 m., C13C, on coral.

Marche–Marchad Coll. 1B, Sud de presque l'île du Cap Vert, 18.ii.54, 46–50 m. 4D, Cap Matakong, Guinée Ise, on shell, with many other species. 16P, either S.W. Madeleines, 15.ix.53, 48 m., or Sud de Gorée, 13.xi.53, 34–37 m., on *Cleidochasma oranense*; 23M, Drag. 1, 18.ii.54, no other information. 30F, Sud de presque l'île du Cap Vert, 18.ii.54, 95 m.

Achimota Coll. Stn. O, Dredged shingle, 8 fath., 2 miles off Densu, Accra, 8.iv.49, 64H, on *Cleidochasma oranense*. Stn. 47, Dredge 1, 4.i.51, 44 m., 14R (ancestrula). Stn. 117, Trawl 2, v.4.51, 64 m., 32P and Coll. II, 13K. Achimota, July, 1947, no other information, C, B, on *Cleidochasma oranense*.

Copenhagen Museum. "Galathea" Stn. 4, 22° 19′ N., 17° 05′ W., 2.xi.50, 62 m., 96B. "Atlantide" Stn. 75, 4° 44′ N., 1° 36′ W., 23.i.46, 46 m., 5C. Stn. 145, 9° 20′ N., 14° 15′ W., 13.iv.46, 32 m., 7H, 110E. Stn. 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m., 44L, 45H, 107C. Stn. 141, off Freetown, 9.iv.46, 15 m., 109B. Also at Stn. 133.

British Museum. Capo Blanco, west Africa, 11–35 fath., 1921.5.23.8. Galapagos, 33.5 fath., 1933, 12.10.3. Canu & Bassler Coll. Gulf of Guinea, 1964, Redier Coll.

The great majority of the specimens are plurilaminar, and many encrust large, erect, worn colonies of other Polyzoa, notably those of *Cleidochasma oranense* (Waters).

Dimensions. Holotype. Lz 0·40–0·50 mm., lz 0·30–0·35 mm., L or 0·05–0·07 mm., l or 0·15–0·17 mm., av. L distal av 0·08 mm., Lm 0·04 mm., av. L lateral av 0·15 mm., l m. 0·07 mm.

West African specimens. Lz 0·35–0·60 mm., lz 0·30–0·42 mm., L or 0·06–0·11 mm., l or 0·10–0·14 mm., av. L distal av 0·05 mm., Lm 0·03 mm., L lateral av 0·10–0·23 mm., Lm 0·05–0·17 mm.

Zoarium encrusting, plurilaminar. Zooids with a horse-shoe shaped orifice, and a raised peristome. Frontal pores stellate. Large, paired lateral-oral avicularia present, with occasionally one small, distal avicularium. Mandibles acute, curved, directed proximally in the distal avicularium, and distally, round the sides of the peristome, or toward the orifice, in the lateral avicularia. Diatellae present. Ovicells not known.

Triporula manica was described (as *Enantiosula*) by Canu & Bassler (1930 : 23) from the Galapagos Islands, from 33·5 fath. The species was defined as having two avicularia, but Osburn (1952 : 469) pointed out that a third, small, distal avicularium was often present, although it might be vestigial and replaced by a pore. The zooids of Osburn's specimens were larger than those of *T. stellata*, but those of a paratype specimen (Galapagos, Stn. D2815, 33·5 fath., 1933. 12. 10. 3, Canu & Bassler Coll.) are very similar (Lz 0·40–0·50 mm., lz 0·30–0·40 mm., Lor 0·10–0·14 mm., lor 0·12–0·16 mm., L lat. avic. 0·10–0·18, Lm 0·08–0·15 mm.).

Smitt (1873) described the differences in appearance produced by secondary calcification. At the growing edge, the operculum is just visible, the avicularia are distinct, and the pores large and stellate. As calcification proceeds the orifice becomes tubular, then immersed. The avicularian rostra also becomes less obvious, and the pores may be occluded. The distal avicularium, which was described by

Smitt, is frequently replaced by a small pore, and even when present, is always small, and is soon immersed by secondary calcification.

The position and size of the lateral avicularia is variable. Those figured by Smitt are small, and directed toward the proximal border of the orifice. They should be compared with those in the photograph of his specimen (pl. 2, fig. B), which show the effects of secondary calcification, and are frequently directed almost vertically. In the west African material, the avicularia are generally large, and directed towards the distal border of the orifice, as in " *E. manica* ". The distal ends of the rostra nearly meet in some specimens. It is noticeable that in hollows in the colony, and on the concave sides of shells, the avicularia are very large, and the rostra raised, obscuring the sides of the orifices. In other parts of the colony, and in some entire specimens, the avicularia are, however, much smaller (as in specimen Achimota C, B), and resemble Smitt's figures.

Specimens from the Gulf of Mexico (" Cavalier " Stn. 311, Lagaaij Coll.), which I have examined are very similar in character to those from west Africa. Three avicularia are usually present, the rostra of the lateral pair extending at least halfway up the sides of the orifice. The frontal pores vary in development from irregular foramina to stellate pores.

HIPPOPETRALIELLA Stach

Hippopetraliella Stach, Harmer, 1957 : 700.

Hippopetraliella africana n. sp.[6]

(Plate 1, fig. C)

HOLOTYPE, B. M. Achimota Coll., Stn. G, 38D, figured specimen.

MATERIAL EXAMINED. Achimota Coll. Stn. E, Christiansborg shore, 15.i.49, 34D; Stn. F, as above, 14.ii.49, 11B; 13A; Stn. G, as above, 19.xi.49, 38D; Stn. U, Tenpbobo shore, 13.ii.49, 67C; Stn. 47, Dredge 1, 4.i.51, 44 m., 14G; Stn. 69, Dredge 5, 22.1.50, 22 m., (dead).

H. africana is not present in the " Calypso ", Marche–Marchad or " Atlantide " Collections.

DIMENSIONS. Lz 0·90–1·20 mm., lz 0·43–0·82 mm., Lo 0·23–0·27 mm., lo 0·22–0·25 mm., Lop 0·22–0·25 mm., lop 0·22–0·23 mm., Lav 0·10–0·27 mm., Lm 0·05–0·12 mm., Lov 0·41–0·50 mm., lov 0·40–0·45 mm.

Zoarium unilamellar, loosely encrusting, with erect expansions. Orifices elongated, with a pair of oral condyles. Operculum with an incomplete proximal sclerite. Ovicells globose, prominent, minutely porous. Avicularia oral, frequently paired, with a complete bar, directed laterally. Basal surface with from one to five multiporous rootlet plates per zooid, frequently very large, surrounded by a raised rim.

The frontal shield develops in the typically umbonuloid manner described by Harmer for the Ascophora Imperfecta.

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[6] Named as the first representative of the genus from west African waters.

H. africana has many characters similar to those of *H. dorsipora* (Busk). The zooids are slightly larger, but the small oral avicularia are of a similar size and shape. The mandible has, however, no teeth as are found in *H. dorsipora*. Occasionally, larger, more elongated avicularia, directed distally, are present; they have a rounded mandible with a strong central sclerite. The ovicells are more prominent than those of *H. dorsipora* and have a raised proximal rim. *H. africana* also differs in that the orifice is longer than wide, and the operculum has an incomplete proximal sclerite. The basal rootlet plates are very large, some almost covering the entire basal wall.

H. africana differs from both *Petraliella bisinuata* and *P. marginata* Canu & Bassler (1928*a* : 78, 80, Gulf of Mexico) in its smaller, rounder avicularia, and lack of any serration on the proximal rim of the orifice.

H. africana is a shallow water species, distributed from the littoral region to 44 m. It is the only representative of the family so far recorded from west Africa. Harmer (1957 : 694) noted that no species belonging to the Petraliellidae had been described from the Atlantic. *Utinga castanea* (Busk) has been recorded from Brazil, see Marcus (1949 : 19); it differs from *H. africana* in the shape of the orifice, in the distribution of the avicularia, and in the size of the basal rootlet pores.

METRARABDOTOS Canu

Metrarabdotos Canu, 1914 : 472; Buge & Galopim de Carvalho, 1963 and 1964.

Brown (1958 : 64) showed that *Metrarabdotos* is not a synonym of *Trigonopora*, as was stated by Canu & Bassler (1935 : 53). The genus has been discussed recently by Buge (1957, as *Trigonopora*), and Buge and Galopim de Carvalho (1963 and 1964). The great majority of the species is known only from fossil deposits.

Metrarabdotos unguiculatum Canu & Bassler[7]

(Plate 1, fig. D)

Metrarabdotos unguiculatum Canu & Bassler, 1929a : 128, pl. 23, figs. 6–9, text-fig. 26, Yucatan, Gulf of Mexico, Straits of Florida, coral and sand, 21–56 fath. 1928c : 92, pl. 8, fig. 9, Brazil, 49 m. Calvet, 1931 : 112, Cape Verde Islands, 91 m. Redier, 1965 : 388, Gulf of Guinea, 70 m., mud, sand, shell, gorgonids.

Trigonopora unguiculatum (Canu & Bassler) Marcus, 1955 : 304, pl. 6, fig. 70, Brazil, 35 m.

Metrarabdotos unguiculatus (sic) Canu & Bassler, Buge & Galopim de Carvalho, 1963 : 181, figs. 23–24. 1964 : 656.

MATERIAL. " Calypso " Coll. I. Stn. 25, 4° 36′ 5″ N., 1° 31′ W., 24.v.56, 50 m., C10S, on stone. Coll. II. Stn. 75, 16° 04′ 20″ N., 22° 58′ 10″ W., 25.xi.59, 45 m., C103A, on Echinoderm test.

Marche–Marchad Coll., I. Sud de Gorée, 24.xi.53, 40–41 m., 11A; S.W. de Madeleines, 9.i.54, 45–46 m., 26A; as above, 15.ix.53, 48 m., 24A. Col. II.; S.W. Madeleines, 15.ix.53, 48 m., 40B; Sud de Gorée, 27.x.53, 38–42 m., 41A; as above, 13.xi.53, 34–37 m., 43A.

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[7] Dr. A. C. Cheetham, who is currently revising this genus, has examined specimens from west Africa and informs me (*in litt* 1.iii.67) that he considers them to be distinct from *M. unguiculatum s s.*

Achimota Coll. Stn. L, dredge in 4 fath., 2 miles W. of Densu, 1 mile offshore, 2.iii.49, 27B; Stn. O, off Densu River, 8 fath., 8.iv.49, 64I, 84IB + 15B (Coll. II); Stn. W, Apam shore, 3.iv.50, 66A; Stn. 47, dredge 1, 4.i.51, 44 m., 14f; Stn. 48; dredge 2, 4.i.51, 44 m., 22D, 46N., on *J. foetida*, 63C; Stn. 117, Trawl 2, 5.iv.51, 64 m., 32B. Coll. II, Chorkor shore, 22A, on stone.

Copenhagen Museum. " Atlantide " Coll. Stn. 75, 4° 44′ N., 1° 36′ W., 23.i.46, 46 m., 5A 41A, 64B. Stn. 85, 5° 37′ N., 0° 38′ E., 30.i.46, 28–50 m., 108D. Stn. 145, 9° 20′ N., 14° 15′ W., 13.iv.46, 32 m., 44K, 110C. Stn. 146, 9° 24′ N., 14° 48′ W., 13.iv.46, 50–51 m., 45F, 107K. Stn. 147, 9° 28′ N., 14° 58′ W., 14.iv.46, 45 m., 77G.

British Museum. Gulf of Bahia, 1899. 5. 1. 792, (as *Lepralia areolata*). Hincks Coll; John Adams Bank, off Brazil, 1899. 7. 1. 529, 5298, Busk Coll; Victoria Bank, off Brazil, 1854. 11. 15. 325–331 pt., Brit. Mus. Cat. Coll. Gulf of Mexico, Albatross Stn. 2405, 30 fath., sand, 1932. 3. 7. 81, Canu & Bassler Coll; MB1/A1 C, Longhurst Coll.

DIMENSIONS. Lz 0·76–0·93 mm., lz 0·42–0·67 mm., Lo (secondary) 0·22–0·25mm, lo 0·17–0·22 mm., Lav 0·21–0·41 mm., Lm 0·17–0·32 mm., Lfz 0·94–1·20 mm., Lov 0·41–0·59 mm., lfo 0·45–0·56 mm.

Zoarium erect, tubular, arising from an encrusting base, usually violet or purple in colour, even when preserved. Zooids with conspicuous marginal pores, bordered by ridges, and 5–7 lateral and 1–2 distal multiporous septulae. Orifice with a raised peristome, which has a proximal sinus and a channel running down inside to the operculum. Avicularia lateral-oral, replacing marginal pores. The rostrum acute, curved, directed distally, and the mandible running up the side of the peristome, curving into the secondary orifice. Ovicells enormous, with a porous frontal and large marginal pores; orifice very wide, slit-like, proximal lip everted and thickened.

M. unguiculatum is one of the most easily recognizable of all the species from west Africa. The large, erect, tubular zoaria, and the purple colour, make it possible to distinguish it in samples with the naked eye. The colour is principally provided by the thick cuticle covering the zooid, and by the polypides and frontal membranes. The cuticle is also frequently covered by a layer of diatoms in specimens from both sides of the Atlantic (see also Marcus, 1955 : 304). The specimens Achimota Coll. II, 22A and " Calypso " Coll. C 103A, are encrusting and plurilaminar. The colour is pale pink, and the avicularia and zooids are slightly smaller (on average) than those of the erect specimens.

The frontal shield develops in the umbonuloid manner (see p. 324). The large marginal pores are at first conspicuous, but as the shield develops they become bordered by ridges of calcification which raise the level of the margins of the zooids laterally and proximally. The funnel-shaped openings between the ridges then become tuberculate. The primary orifice is rounded and slightly elongated. As the peristome develops a pair of processes delineate a rounded sinus proximally at its base. The processes extend with the upward growth of the peristome, forming a channel, and also produce a proximal sinus in the secondary orifice.

The relationships of the frontal membrane and operculum have been described, for *M. gulo* (see below), by Marcus (1955 : 304). Dissection of these specimens has shown that in *M. unguiculatum* there is no well defined operculum. A thickened, semicircular, flap-like extension of the frontal membrane protrudes into the base of the peristome. It is attached laterally by muscles inserted into the lateral walls of the base of the peristome.

Although both Canu & Bassler and Buge & Galopim de Carvalho have described small avicularia at the edges of the orifice of the fertile zooids, none have been seen in any of the material listed above. An enlarged marginal pore is, however, frequently present. The embryos of *M. unguiculatum* are very large (average dimensions Le 0·45 mm., le 0·37 mm.).

Apart from Buge & Galopim de Carvalho's mention of an unnamed Recent species from the Eastern Atlantic (1963 : 187), the only Recent record attributed to *M. unguiculatum* from the west African coast before that of Redier (1965) was that of Calvet (1931 : 112), who listed it from the Cape Verde Islands (91 m., on *Lithothamnion*). This is remarkable, as *M. unguiculatum* is a robust and easily recognizable species, which occurs in these Collections in large quantities. Canu & Bassler 1925 and 1928*b*) did not, however, find it in their Moroccan material, and its distribution appears not to extend further north than the Cape Verde area.

Marcus (1955 : 304, pl. 6, figs. 71–72, pl. 7, figs. 73–77) described, as *Trigonopora gulo*, a Recent species from Brazil (Espirito Santo, 35 m.). The avicularia were either small, or large, with bifurcate mandibles, there were none present on fertile zooids. Buge & Galopim de Carvalho did not include *M. gulo* in their survey of the genus. It seems possible that *M. tuberosum* Canu & Bassler (1928*c* : 92, pl. 8, figs. 3, 4, off Brazil, 36 m.), which was figured with small avicularia, may be closely related to *M. gulo*. Canu & Bassler (1928*c* : 92, pl. 8, fig. 9, Brazil, 49 m.), also recorded *M. unguiculatum*, and the majority of specimens in the British Museum Collection is from the same area (see above).

M. unguiculatum appears to be associated with moderately deep water, and sandy sea bottoms. Lagaaij noted (1952 : 124, footnote), that the distribution of his *Trigonopora nysti* in sand and clay deposits, seemed " to indicate a rather deep-water facies ". The species described by Lagaaij under *Trigonopora* are all referable to *Metrarabdotos* (see Brown, 1958 : 64). The specimens from shallow water in the west African Collections are usually dead and worn, the remaining specimens are from 34–64 metres. Several of the Achimota Collection Stations at these depths are in or near the area of the " silty sand community " defined by Buchanan (1958). The majority of the specimens comprises broken fragments, but two show evidence of the mode of growth. " Calypso ", C10S encrusts a stone, but includes the base of an erect, tubular branch. Achimota 46N is another erect fragment growing from a base which encrusts a fragment of *Jullienella foetida*. *J. foetida* is a Foraminiferan with an argillaceous test which forms large foliaceous colonies. It is one of the dominant forms of the silty sand community off the coast of Ghana (see Buchanan, 1958, and also Nørvang, 1961).

SUMMARY

Five species of *Cellaria* are described from the west African region, one of which

is considered to be new. Only three species belonging to the Cribrimorpha have been found from the area. One, *Membraniporella marcusi*, from west Africa and Brazil, is here considered to be distinct from *M. aragoi*, a similar species which occurs in the Red Sea and the Gulf of Mexico. The Division Ascophora Imperfecta comprises two distinct groups of genera, which differ in the method of development of the frontal shield. Both groups are represented from west Africa. The first, in which the shield is formed from the anastomosis of spinous processes, and is similar to that found in the Cribrimorpha, includes species of *Tremogasterina*, *Exechonella* and *Triporula*. The second, in which the shield develops in the umbonuloid manner described by Harmer (1957), includes species of *Hippopetraliella* and *Metrarabdotos*.

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PLATE 1

Membraniporella, Hippopetraliella, Metrarabdotos and *Exechonella.*

FIG. A. *Membraniporella aragoi* (Audouin). Florida, 1965. 8. 6. 2., Maturo Coll. Zooids and ovicells. ×16.

FIG. B. *M. marcusi* n. sp. 59H, Achimota Coll., Ghana. Zooids and ovicells, note ancestrula. ×13.

FIG. C. *Hippopetraliella africana* n. sp. 38D, Achimota Coll., Ghana. Zooids and ovicells. ×16.

FIG. D. *Metrarabdotos unguiculatum* Canu & Bassler. 32B, Achimota Coll., Ghana. Part of a tubular branch, showing zooids with avicularia, and two ovicells. Note the umbonuloid development of the frontal wall of the distal zooids, and, proximally, one partially developed, aborted ovicell. × 11.5.

FIG. E. *Exechonella antillea* (Osburn). 65C, Achimota Coll., Ghana. Zooids showing slightly raised peristomes and large frontal foramina. × 20.

Figures A–D photographed by Mr. H. V. Christensen (Zoologisk Museum, Copenhagen), figure E photographed by Mr. J. V. Brown (British Museum, Natural History).

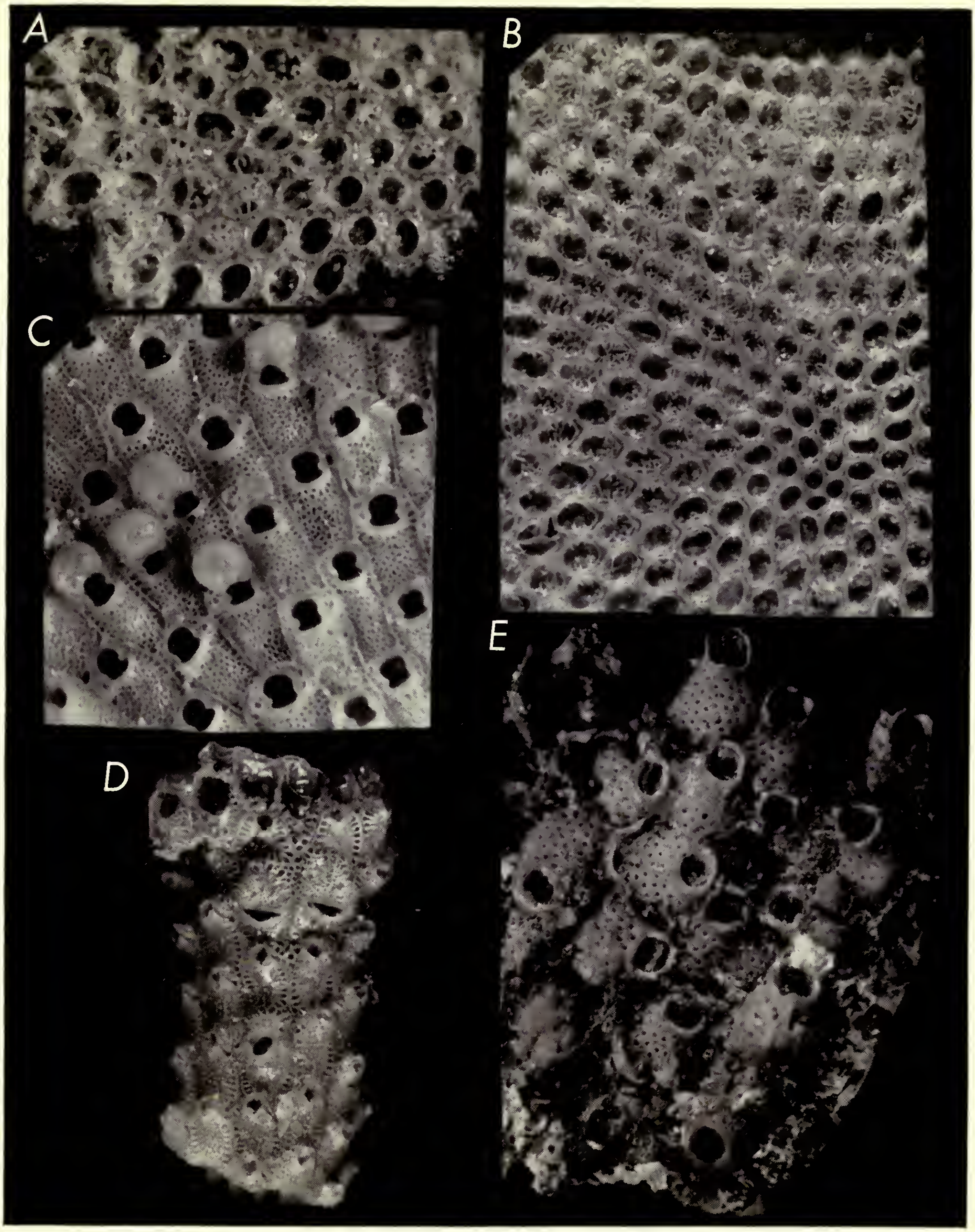
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PLATE 2

Triporula and *Exechonella*.

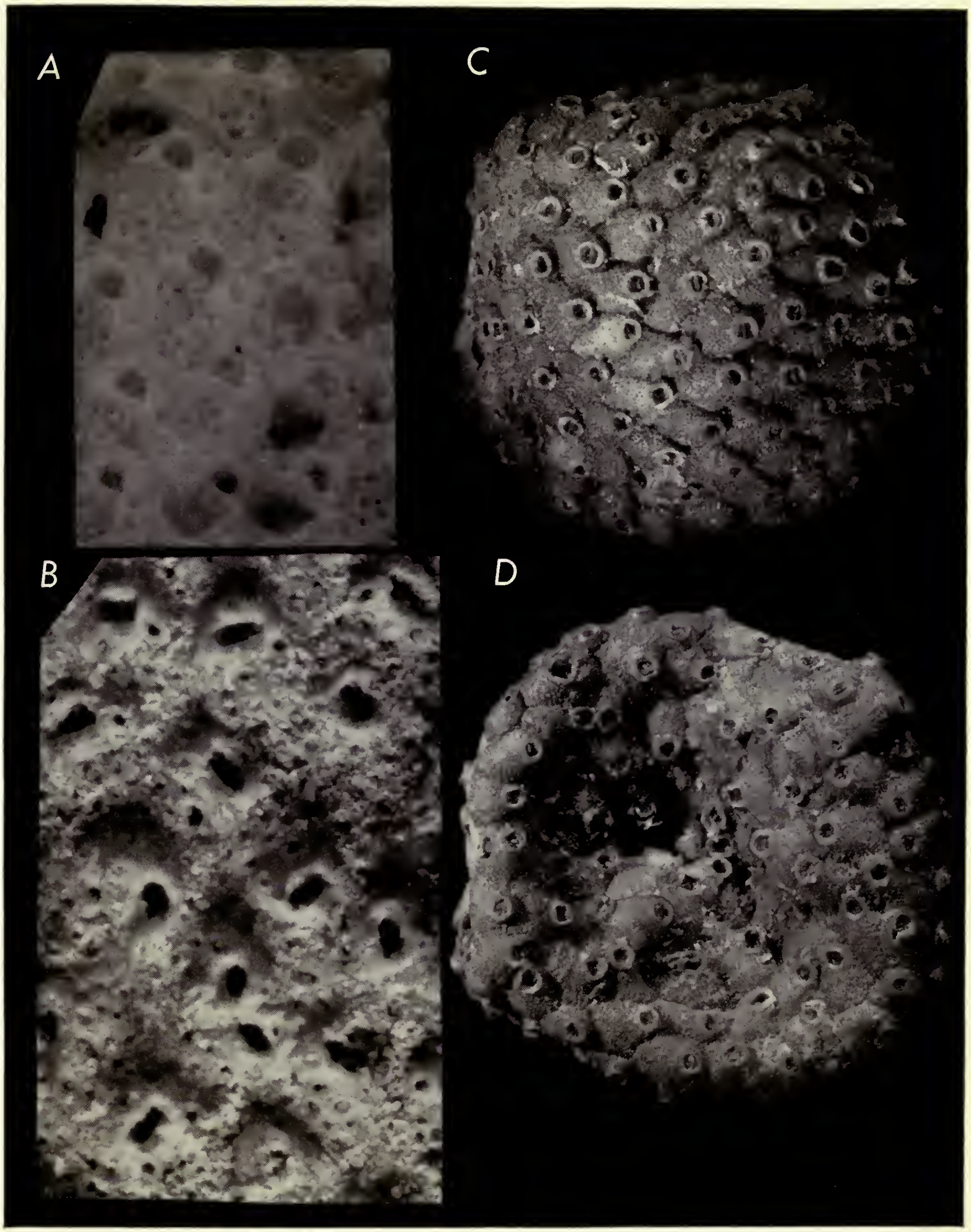
Fig. A. *Triporula stellata* (Smitt). "Atlantide" Stn. 133, Angola, Zoologisk Museum, Copenhagen. Zooids and avicularia. Note developing frontal shield of the distal (left-hand) zooid. × 43.

Fig. B. *T. stellata*. S.W. of Tortugas, 60 fath., Pourtales Coll., No. 218, No. 1805, Naturhistoriska Riksmuseet, Stockholm. Zooids and avicularia. Note the difference in appearance of the zooids resulting from secondary calcification. × 55.

Fig. C. *Exechonella gigantea* n. sp. Marche–Marchad Coll. I, 11 J, Senegal. Holotype Convex face. of zoarium. Note the short, thickened peristomes. × 8.

Figs. D, E. The same specimen. Concave face of zoarium. Note the prominent peristomes at the centre of the colony. Composite picture taken at two levels of focus. × 8.

Photographs by J. V. Brown.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BRADY, 1899
(CALIGIDAE: COPEPODA)

R. R. PARKER

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BY

R. R. PARKER

Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

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This paper is Vol. 15, *No.* 8 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

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CALIGUS LONGICAUDATUS BRADY 1899 (CALIGIDAE: COPEPODA)

By R. R. PARKER

INTRODUCTION

In 1899 Brady described and illustrated a single specimen of *Caligus* obtained in a surface plankton-net tow at Port Chalmers, New Zealand. Both his description and figure were inadequate for identification of the species; the figure erroneously depicted the 2nd antennae and omitted the sternal furca and 1st thoracopods, etc. One cannot be certain even of the sex although Hewitt (1963), who further described the species from Brady's figure, thought the specimen to be a male. Aside from a listing by Hutton (1904), the binomen had not been mentioned again in the literature until 1963. Cleugh (1966) disagreed with Hewitt's proposal for a new name and argued that the name *C. longicaudatus* Brady was valid; but he called attention to the facts that the species was founded on a single specimen, was inadequately described, and required validation.

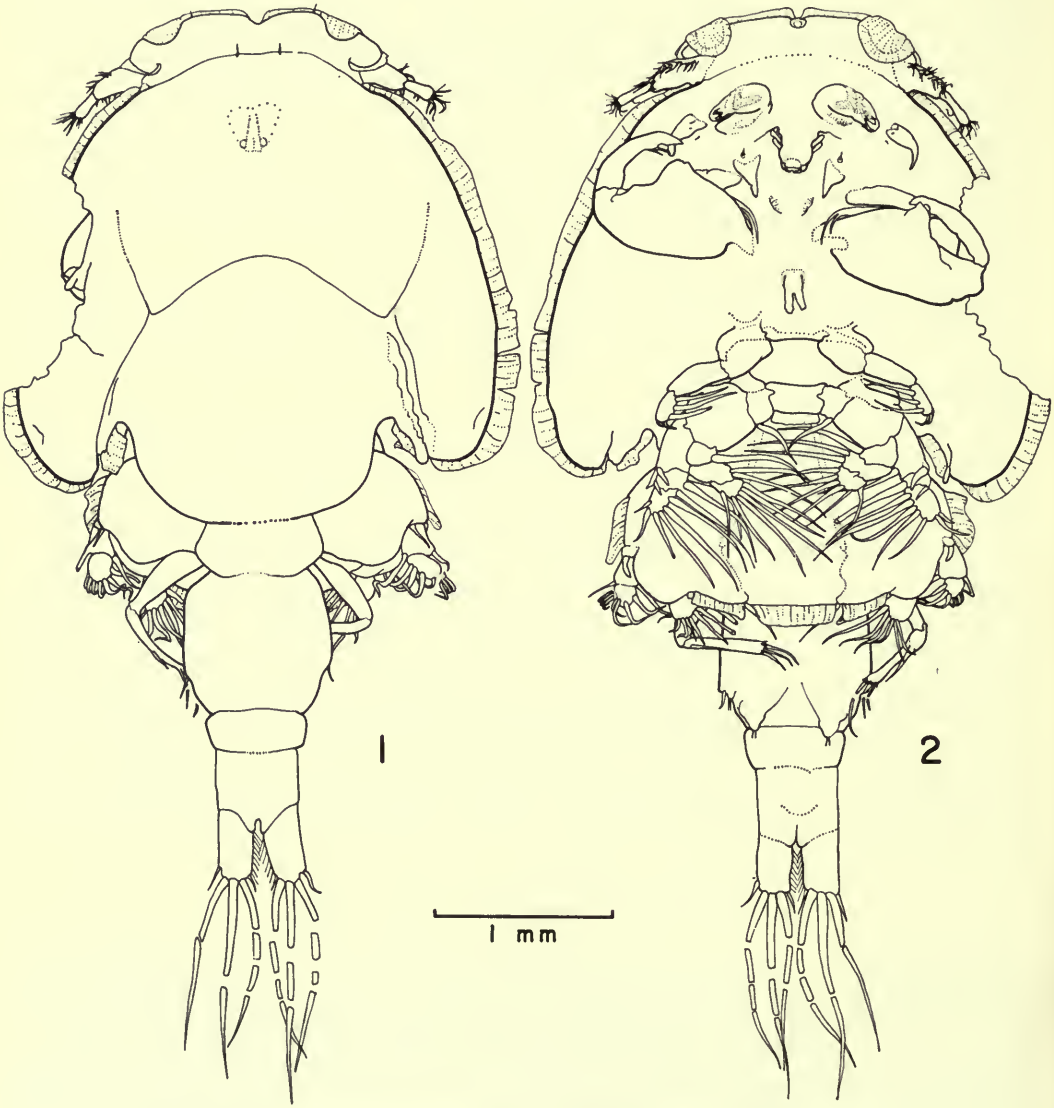
A letter to Dr. J. P. Harding quickly established that Brady's specimen existed in the British Museum (Natural History). Through the efforts of Miss Patricia Lofthouse, Entomostraca Section, the Trustees of the Museum kindly loaned Brady's specimen for examination.

The specimen was mounted, ventral side up, on a glass slide. The cover slip was crazed, having been supported by the large maxillipeds while the mountant had shrunk. The specimen could not be examined in that condition. From the report by Stock (1960) it was learned that Brady's specimens were usually mounted in a glycerin–gelatin medium and could be recovered by soaking in water. (Dr. Stock's description of the state of the mounted specimens aptly applies in the present case.) Thus it was possible to recover the specimen, which was severely damaged, and by clearing with lactic acid, to redescribe it. The specimen was drawn in detail, using a camera lucida, by Miss Margaret Dean of this laboratory. I am also indebted to Dr. Z. Kabata and to Dr. L. Margolis for consultation in this project. The specimen has been returned to the British Museum (Natural History), as No. 1951.8.10.141 Type, in ethanol. The following redescription presents all of the detail which could be discerned from the type specimen. I have deliberately presented a very brief verbal account, relying upon the figures for anatomical detail.

Caligus longicaudatus Brady, 1899

The specimen is a male. Exclusive of the terminal spines of the caudal lamellae the total length was 4·93 mm, (Brady gave 5 mm.). From the dorsal aspect (Text-fig. 1) the carapace length including the frontal lobes is 58% the total length or approximately 2·84 mm. The maximum width of the carapace measured 2·93 mm., however the specimen was severely flattened in its former mount and did not regain its original shape. The dorsal surface of the carapace was marked with scattered minute branched cilia, positioned in a bilaterally symmetrical pattern. Their function is unknown to me. Similar cilia also were found on the dorsal surface of the 3rd thoracopods, the 4th and genital segments, and the abdomen. The abdomen is of 2 segments, the anterior being slightly wider but about half the length of the posterior segment. The caudal lamellae bear the usual 3 small and 3 large ciliated setae (cilia not shown) and the entire medial edge of each lamella is ciliated.

From the ventral aspect (Fig. 2) the lunules appear semi-circular and prominent.



FIGS. 1–2. *Caligus longicaudatus*. 1. Dorsal view. 2. Ventral view.

The frontal plates are about 0·23 mm. long and are bordered by a hyaline fringe broken at the midline by the embryonic cement gland.

Cephalic appendages are shown in larger detail in Text-figs. 3–9. *Antennules* (Text-fig. 3) are composed of 2 segments. The basal segment bears 25 spines ventrally and 2 spines dorsally which are arranged along the lateral edge. Twenty-three of the ventral spines are definitely ciliated (cilia not illustrated). The remaining 2, situated at about mid-length, are thought to be naked. The 2 dorsal spines are ciliated. The tip of the distal segment bears 13 naked spines, 2 of which appear to have a common base. A 14th naked spine originates from the medial edge at about mid-length of the segment. As is shown in Fig. 3, the spines of the basal segment are of variable lengths, but are relatively long for members of this genus; 2 spines originating from the distal edge project nearly to the tip of the distal segment. *Antennae* (Text-fig. 4) are modified as is usual for the male and are composed of at least 3 segments (a basal segment may be incorporated into the ventral cephalic surface). The first and second segments are sculptured with adhesion pads. The distal segment is modified into a small claw which bears a fine membrane along each edge. Originating with these membranes are 2 accessory spines.

The *post-antennary* process (Text-fig. 5) is strongly developed, slightly hooked and pointed. Two papillae on the base give rise to hair-like setae and a third papilla near the base gives rise to an additional hair-like seta.

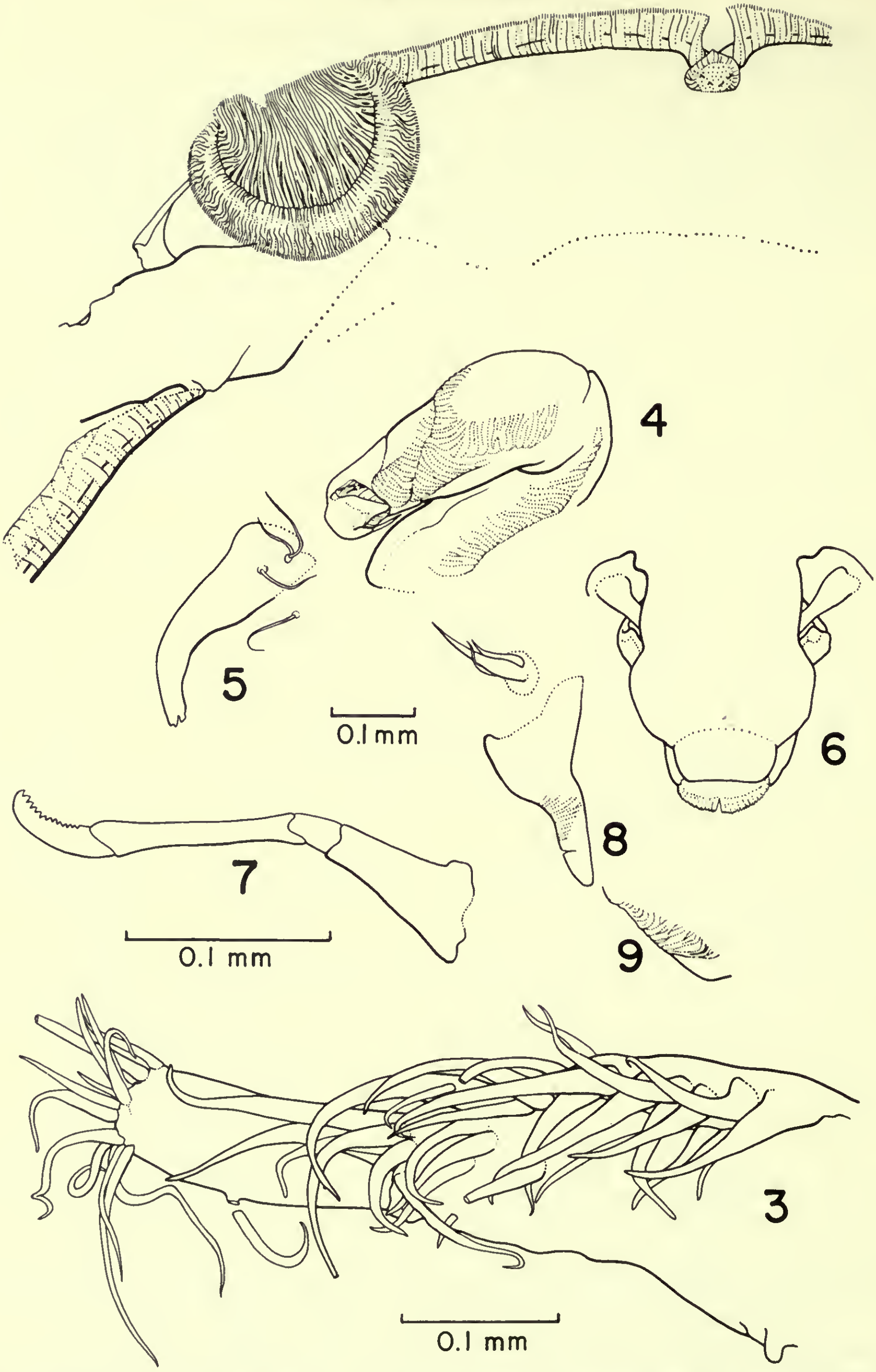
The *mouth cone* (Text-fig. 6) is the usual tube-within-a-tube structure with the mandibles entering mandibular tubes (formed by involutions of the ectoderm) near the base of the mouth cone. The mandibular tubes penetrate the mouth cone distally, thus separating the cone into dorsal and ventral flaps. A circular flap, apparently separated from the ventral flap proper, extends the ventral region of the mouth cone and is bordered distally by a fringed membrane. A similar membrane is thought to border the dorsal flap.

Mandibles (Text-fig. 7) are composed of 4 segments; the distal segment bears 12 teeth on the medial edge.

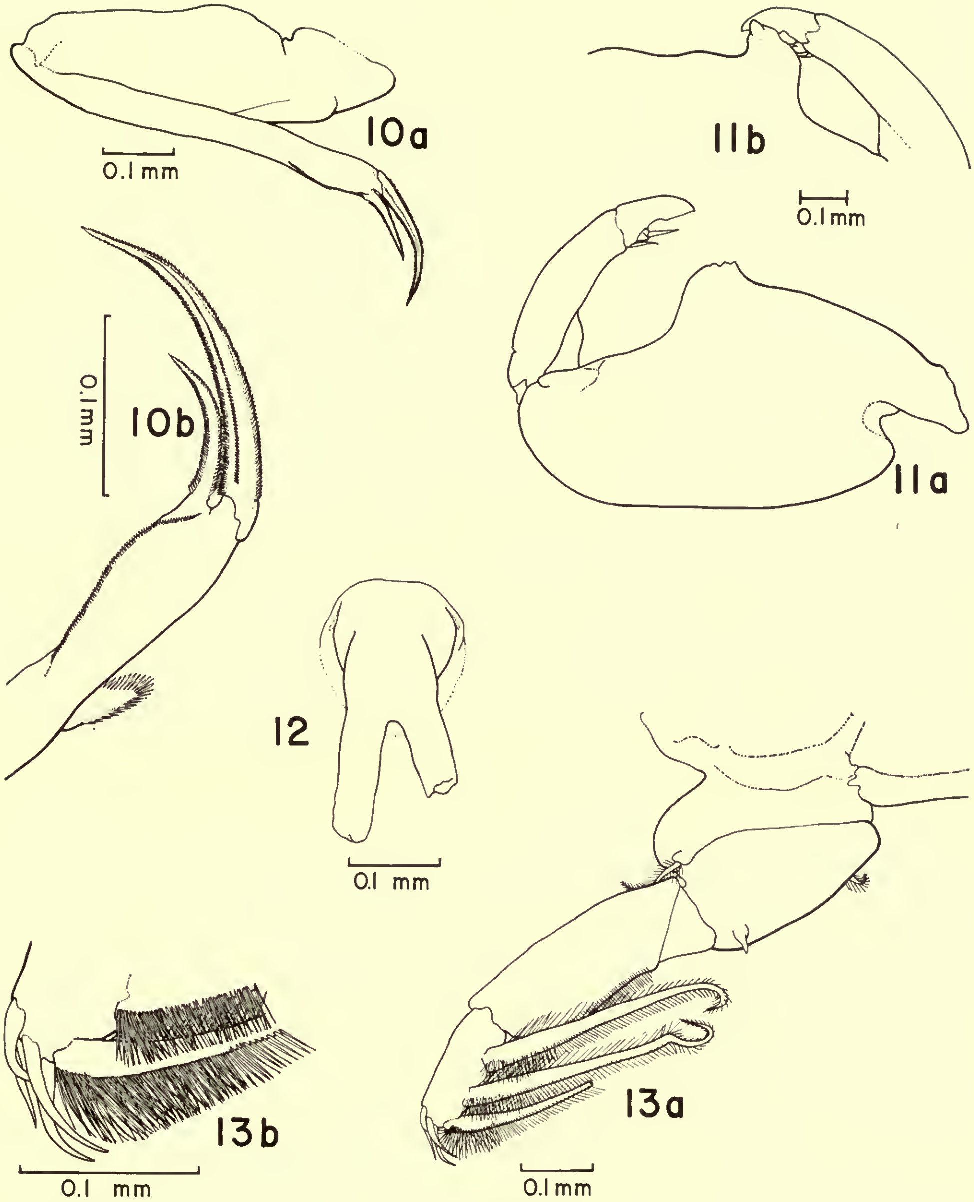
The *maxillules* (Text-fig. 8) are largely incorporated into the ventral integument. Anteriorly a papilla bears 3 flattened spines of dissimilar lengths. Posteriorly the maxillule is represented by a prominent heavy spine. Faint striations were seen on the distal half along the ventro-lateral edge. Posterior to the maxillules are a pair of adhesion pads (Text-fig. 9) which may be of taxonomic significance.

Maxillae (Text-fig. 10a, b) are interpreted to be composed of 4 segments. The basal segment is short and heavy, followed by an equally thick but long second segment. The 3rd segment is long and slender and bears the usual fringed lappet about two-thirds the segment length distally. In addition, a clearly defined fringe extends from this lappet distally to the base of the fourth segment. The laterodistal corner is extended into a prolonged pointed extension, fringed along both borders. The 4th segment is nearly one-third the length of the third segment, tapers to a point and bears 3 definite rows of cilia along its length, possibly a fourth row dorsally, which are so spaced to divide the circumference into 4 equal parts.

The *maxillipeds* (Text-fig. 11a, b) are strongly developed, as is usual for males of the genus. The medial edge is developed into a protruding rough spine into which the



FIGS. 3–9. *Caligus longicaudatus*. 3. Right antennule, ventral view. 4. Right antenna, *in situ*, ventral view. 5. Right post-antennary process, *in situ*, ventral view. 6. Mouth cone, *in situ*, ventral view. 7. Left mandible, ventral view as seen in the mouth cone. 8. Maxillule, *in situ*, ventral view. 9. Adhesion pads, *in situ*, ventral view.
FIGS. 4, 5, 6, 8 and 9 are depicted in positional relationship to the frontal membrane and and lunule show above them as seen from ventral view.


10a
0.1 mm
11b
0.1 mm
0.1 mm
10b
11a
12
0.1 mm
13b
0.1 mm
13a
0.1 mm

FIGS. 10a–13b. *Caligus longicaudatus.* 10a. Right maxilla, ventral view. 10b. Enlargement of apical end of left maxilla, ventral view. 11a. Right maxilliped, ventral view. 11b. Portion of left maxilliped, ventral view. 12. Sternal furca, ventral view. 13a. Right 1st thoracopod, ventral view. 13b. Enlargement of apical portion of right 1st thoracopod.

tip of the maxilliped fits when closed. The 2 distal segments together form a claw. At the suture line, on the distal segment, are located 2 small spines. The distomedial edge of the apical segment is sharp, resembling the blade of a knife.

The *sternal furca* (Text-fig. 12) of the specimen is damaged, however the right prong is flattened and slightly spatulate at the tip.

The *1st thoracopods* (Text-fig. 13a, b) consist of a 2-segmented protopod and a 2-segmented exopod. The endopod is represented by a small papilla projecting into a minute spine. The 4 apical spines of the distal exopodal segment are unbranched and apparently naked.

The *2nd thoracopods* (Text-fig. 14) consist of a 2-segmented protopod, and 3-segmented exopod and endopod.

The *3rd thoracopods* (Text-fig. 15) are not unusual. The heavy spine on the 1st exopodal segment is flattened, curved, with a knife edge laterally. Dorsally, a small, ciliated (cilia not shown Text-fig. 1) spine originates from the protopod and projects over the base of the exopod.

The *4th thoracopods* (Text-fig. 16) are composed of 3 segments; the lateral edge of the distal segment does not posess a spine. The apical spines of the 2nd and 3rd segments are finely ciliated along both borders. Those of the 3rd segment are covered at their bases by finely pectinated lamellae.

The *5th thoracopods* (Text-fig. 17) are represented by 2 papillae, the lateral one bears a single ciliated spine, the medial papilla bears 2 similar ciliated spines.

The *6th thoracopods* (Text-fig. 17) are found caudally on the ventral surface of the genital segment. They consist of a pair of caudally projecting lobes terminated by 2 ciliated spines. A small naked spine is located on the genital segment between the 5th and 6th thoracopods.

DISCUSSION

While Brady's name *C. longicaudatus* is available for his specimen it remains to be determined if the species was described prior to 1899[1] under another name. According to our records there were 108 species named to the genus prior to that date. Of these 32, as listed in Table I, are recognized as belonging to other genera. Included in this list is *C. lessonius* Risso, 1826, described as possessing foliaceous plates attached to the first 2 segments of the abdomen. A further 20 species, as listed in Table II, are recognized to be junior synonyms of previously described species. Included here is *C. appendiculatus* F. Müller, 1852, described from a chalimus stage found on *Cyprinus rutilus* on the shore of the Baltic Sea. The binomen was last mentioned by Nordmann (1864), i.e. more than 100 years ago. Therefore, according to Article 23(b) of the International Code of Zoological Nomenclature (1961), it has no status. It is obvious, however, that Müller described a juvenile male *C. lacustris* Steenstrup and Lütken, 1861. The male of this species was not figured nor adequately described until Redeke's 1939 paper.

In Table III a list of 13 species names considered *nomina nuda* is presented. Only by examining the type material can the status of these species be established. All

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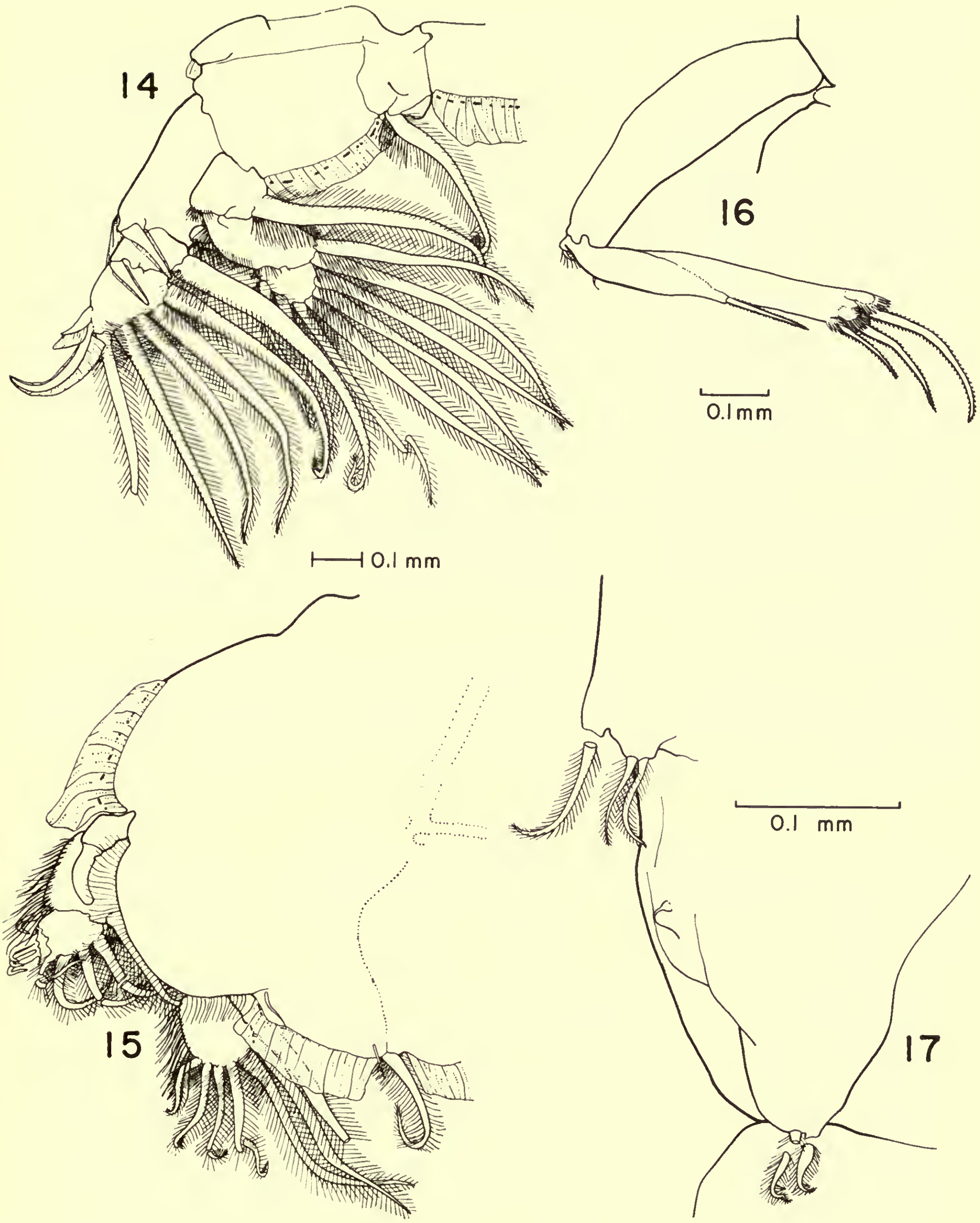
[1] Although 1901 is the commonly quoted date of publication of Brady's paper, it appeared as a separate in 1899 and was bound, with other sections, into a volume issued in 1901.



FIGS. 14–17. *Caligus longicaudatus.* 14. Right 2nd thoracopod, ventral view. 15. Right 3rd thoracopod, ventral view. 16. Right 4th thoracopod, ventral view. 17. Ventral view of left caudal portion of genital segment showing 5th and 6th thoracopods.

but two of the remaining species are grouped in Tables IV to VI according to anatomical features which readily distinguish them from *C. longicaudatus*.

The two species remaining for consideration are *C. lacustris* Steenstrup and Lütken, 1861, and *C. longipedis* Bassett-Smith, 1898c. *C. lacustris* has only been reported from fresh water or from freshwater fishes which have been found in estuarine waters of low salinity. The comparative lengths of the apical spines of the 4th thoracopod are completely dissimilar to those of *C. longicaudatus*. *C. longipedis* also can be separated from *C. longicaudatus* by the relative much longer length of the 4th thoracopods of the former, although the two species are in many ways similar.

It is concluded that *C. longicaudatus* Brady, 1899, is a valid species although known only from a single male specimen taken in a surface townet.

Of the 187 species named to the genus *Caligus* since 1899 there are 162 considered valid members of the genus today. I have compared the descriptions of these species with *C. longicaudatus* and cannot definitely assign any of the former to the latter species. *C. pterois* Kurian, 1949, and *C. debueni* Stuardo and Fagetti, 1960, are so incompletely described that no comparison is possible. *C. brevicaudatus* A. Scott, 1901, and *C. calotomi* Shiino, 1954, are known from females only. These species are similar to *C. longicaudatus* in many morphological details, i.e., thoracopod structure and the sternal furca, yet the gross body proportions may indicate dissimilarity. *C. tetrodontis* Barnard, 1948, is incompletely described. From the details provided by Barnard the species may be identical. These five species are given the status *species inquirenda*.

It is not surprising that *C. longicaudatus* has not been reported since 1899. Relatively little work on the caligids has taken place in New Zealand waters. From the description provided herein it should now be possible to recognize *C. longicaudatus* Brady, 1899, and it should be looked for in the New Zealand fauna.

TABLE I

List of *Caligus* species named prior to 1899 transferred to other genera

Caligus sp.	Author	Transferred by
productus n. sp.	Müller, 1785	Latreille, 1829
crassus n. sp.	Abildgaard, 1794	Krøyer, 1837–1839
oblongus n. sp.	Abildgaard, 1794	Krøyer, 1837–1839
imbricatus n. sp.	Risso, 1816	Desmarest, 1825
piscinus n. comb.	Lamarck, 1818 (in part)	Krøyer, 1837–1839
bicolor n. comb.	Lamarck, 1818	Baird, 1850
smithii n. comb.	Lamarck, 1818	Baird, 1850
heptapus n. sp.	Otto, 1821	Krøyer, 1837–1839
molvae n. sp.	Latreille, 1825[1]	Wilson, 1905
lessonius n. sp.	Risso, 1826	(see text)
paradoxus n. sp.	Otto, 1828	Krøyer, 1837–1839
pharaonis n. sp.	Nordmann, 1832	Humes, 1965
hippoglossi n. comb.	Krøyer, 1837–1839	Baird, 1850
pectoralis n. comb.	Krøyer, 1837–1839	Baird, 1850

TABLE I—*contd.*

Caligus sp.	Author	Transferred by
salmonis n. sp.	Krøyer, 1837–1839	Smith, 1874
sturionis n. sp.	Krøyer, 1837–1839	Wilson, 1905
nordmannii n. sp.	Milne-Edwards, 1840	Baird, 1850
ornatus n. sp.	Milne-Edwards, 1840	Bassett-Smith, 1899
vespa n. sp.	Milne-Edwards, 1840	Baird, 1850
strömii n. nom.	Baird, 1848	Baird, 1850
gracilis n. sp.	Van Beneden, 1851	Carus, 1885
bagri n. sp.	Dana, 1852	Dana, 1853
branchialis n. sp.	Malm *in* Steenstrup and Lütken, 1861	Bassett-Smith, 1899
heckelii n. sp.	Kollar *in* Krøyer, 1863	Krøyer, 1863–1864
macrurus n. sp.	Heller, 1865	Yamaguti, 1963
pacificus n. sp.	Gissler, 1883	Wilson, 1905
brevipedis n. sp.	Bassett-Smith, 1896a, b	A. Scott, 1901
obscurus n. comb.	Bassett-Smith, 1896b	Bassett-Smith, 1899
nautili prov. n.	Willey, 1896	Stebbings, 1900
benedeni n. sp.	Bassett-Smith, 1898a	Bere, 1936
hirsutus n. sp.	Bassett-Smith, 1898a	Wilson, 1912
parvus n. sp.	Bassett-Smith, 1898a	Rangnekar and Murti, 1964

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[1] I have been unable to locate this reference.

TABLE II

List of species names junior in synonomy within the genus *Caligus* (prior to 1899)

Caligus sp.		Authority
mülleri n. sp.	Leach, 1816	Krøyer, 1837–1839
piscinus n. comb.	Lamarck, 1818 (in part)	Krøyer, 1837–1839
bicuspidatus n. sp.	Nordmann, 1832	Nordmann, 1832
americanus n. sp.	Pickering and Dana, 1838	Steenstrup and Lütken, 1861
minutus n. nov.	Krøyer, 1837	Heller, 1866
leptochilus n. sp.	Frey and Leuckart, 1847	Steenstrup and Lütken, 1861
appendiculatus n. sp.	F. Müller 1852	(see text)
elegans n. sp.	Van Beneden, 1851	Steenstrup and Lütken, 1861
coryphaenae n. sp.	Steenstrup and Lütken, 1861	Pillai, 1963
abbreviatus n. sp.	Krøyer, 1863–1864	T. Scott, 1905
aeglefini n. sp.	Krøyer, 1863–1864	Wilson, 1905
carangis n. sp.	Krøyer, 1863–1864	Wilson, 1905
fallax n. sp.	Krøyer, 1863–1864	Dollfus, 1953
lumpi n. sp.	Krøyer, 1863–1864	Olsson, 1869
monacanthi n. sp.	Krøyer, 1863–1864	Wilson, 1905
nanus n. sp.	Krøyer, 1863–1864	Parker, 1965
borealis n. sp.	Olsson, 1877	Markevich, 1956
bengoensis n. sp.	T. Scott, 1894	Bassett-Smith, 1899
scomberi n. sp.	Bassett-Smith, 1896b	Wilson, 1905
longicaudus n. sp.	Bassett-Smith, 1898a	Bassett-Smith, 1899

TABLE III

List of *Caligus* species named prior to 1899 considered *nomina nuda* or *species inquirenda*

Caligus sp.	
scutatus	Milne-Edwards, 1840[1]
cristata	Gould, 1841
gayi	Gay, 1849
gracilis	Dana, 1852
scrombri	J. V. Thompson *in* W. Thompson, 1856
platessae	Van Beneden, 1871
lepidopi	Richiardi, 1880
petersii	Richiardi, 1880
serrani	Richiardi, 1880
smaris	Richiardi, 1880
trachini	Richiardi, 1880
trachuri	Richiardi, 1880
fissus	Richiardi, 1880

[1] The type material is not at the Museum National D'Histoire Naturelle, Paris.

TABLE IV

List of *Caligus* species named prior to 1899 characterized by absence of 3 ciliated spines on medial margin, distal segment of 1st thoracopod (not included in Tables I–III)

Caligus sp.		Spines
productus	Dana, 1852	absent
alalongae	Krøyer, 1863–1864	absent
trichiuri	Krøyer, 1863–1864	present but naked
haemulonis	Krøyer, 1863–1864	absent
affinis	Heller, 1866	absent
dakari	Van Beneden, 1892	absent

TABLE V

List of *Caligus* species named prior to 1899 characterized by 4th thoracopods composed of 4 segments (not included in Tables I–IV)

Caligus sp.	
diaphanus	Nordmann, 1832
thymni	Dana, 1852
isonyx	Steenstrup and Lütken, 1861
chorinemi	Kollar *in* Krøyer, 1863–1864
pelamydis	Krøyer, 1863–1864
constrictus	Heller, 1865
tenax	Heller, 1865
torpedinis	Heller, 1865[1]
trachynoti	Heller, 1865
vexator	Heller, 1865
murrayanus	T. Scott, 1894
arii	Bassett-Smith, 1898b
cybii	Bassett-Smith, 1898a
phipsoni	Bassett-Smith, 1898a
platytarsis	Bassett-Smith, 1898b
robustus	Bassett-Smith, 1898c

[1] Brian, 1924, considered *C. torpedinis* a possible synonym of *C. diaphanus* Nordmann.

TABLE VI

List of *Caligus* species named prior to 1899 characterized by 4th thoracopod composed of 3 segments, with a spine present on lateral edge of the distal segment in addition to 3 terminal spines (not included in Tables I–IV)

Caligus sp.	
elongatus	Nordmann, 1832[1]
kroyerii	Milne-Edwards, 1840[2]
rapax	Milne-Edwards, 1840[2]
rissoanus	Milne-Edwards, 1840[2]
angustatus	Krøyer, 1863–1864
belones	Krøyer, 1863–1864
gurnardi	Krøyer, 1863–1864
stromatei	Krøyer, 1863–1864
trachypteri	Krøyer, 1863–1864
infestans	Heller, 1865
irritans	Heller, 1865
dubius	T. Scott, 1894
cossackii	Bassett-Smith, 1898b

[1] Type material was obtained from Institut für Spezielle Zoologie und Zoologisches Museum, Berlin and examined by the author. This loan was arranged through the kindness of Dr. H. E. Gruner, Humboldt-Universität zu Berlin.

[2] Type material was obtained from the Paris Museum and examined by the author. This loan was arranged through the kindness of Dr. J. Forest, Museum National D'Histoire Naturelle, Paris.

TABLE VII

List of *Caligus* species named prior to 1899 of which the male is characterized by an abdomen composed of a single segment (not included in Tables I–VI)

Caligus sp.	
curtus	O. Müller, 1785
minimus	Otto, 1821
centrodonti	Baird, 1850
balistae	Steenstrup and Lütken, 1861
cheilodactyli	Krøyer, 1863–1864
hyalinus	Chernyavsky, 1868

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